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SYSTEMATIC BEHAVIOR DURING DISCRIMINATION REVERSAL AND CHANGE OF DIMENSIONS[1]

478 Z23

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The present study is a preliminary attempt to determine some of the factors governing systematic behaviors, such as position habits, observed in discrimination learning. Systematic behavior as used in this paper refers to a sequence of choices correlated with one aspect of the stimulus situation regardless of whether or not these choices are correlated with the reward. The present study is concerned with three related aspects of such systematic behaviors: (*a*) It attempts a preliminary answer to the question of whether or not, while the animal is reacting systematically to one set of cues, other aspects of the stimulus situation are essentially nonfunctional in the sense that their correlation or association with behavior remains unchanged by the schedule of reinforcement; (*b*) it seeks to relate the amount and type of systematic behavior found to the number and type of randomly varying stimulus dimensions in the situation; and (*c*) it raises the question of how much of the progressive improvement in discrimination reversal can be accounted for by the differential rates at which these systematic behaviors are eliminated.

The first point above needs some elaboration. Although it bears on the controversy between the continuity and noncontinuity viewpoints toward discrimination learning, the actual design of the experiment is quite different from the usual discrimination reversal study that has been employed in this context (1, 2, 3). The simultaneous discrimination used here employs three different stimulus dimensions: (*a*) right vs. left spatial positions, (*b*) black vs. white brightness differences, and (*c*) high vs. low hurdles. These three pairs of cues are combined randomly from trial to trial with the food reward always correlated with one of these six cues, e.g., black. When an *S* has learned this discrimination, there should be considerable differential habit strength between the black and white but little or none between the two types of hurdles and the two spatial positions.

The reward is now correlated with some cue other than brightness, e.g., high hurdles. During this second discrimination, where a correction procedure is used, the animal receives an equal number of reinforcements and nonreinforcements in the black and in the white as well as in each of the two spatial positions. The assumption is made that according to the continuity hypothesis this equivalent treatment of the two brightness cues should tend to equalize them in associative strength. The test comes on the third discrimination.

If learning the hurdle discrimination has equalized the two brightness cues, it should make no difference to *S* if the reward is now correlated with the black, the positive cue of the first discrimination, or with the white, the negative cue of the first discrimination. Each should be learned at the same rate. If, however, the *S* that returns to the black learns considerably more rapidly than the *S* that must learn the white, it indicates that during the interpolated hurdle discrimination the original discrimination was not equalized or broken down. While not conclusive, this would at least suggest the possibility that while the *S*s were reacting to hurdles in a systematic fashion the black-white cues were largely nonfunctional.

METHOD

Subjects and Apparatus

The *S*s were 48 albino rats approximately 60 days old, divided equally between males and females. The discrimination apparatus consisted of a starting box that led by means of a sliding door into a mesh-covered alley which was 6 in. long, 2½ in. wide, and 4¾ in. high. It opened into the small end of a funnel-shaped compartment 7 in. long and 9 in. in width at its far end. Facing into the broad end of the funnel were two goal boxes each 10 in. long and 4½ in. wide. These were covered by a glass lid and contained sliding doors to prevent retracing. The food cups were countersunk holes at the far end of the goal boxes. The entire apparatus, except for the goal boxes, was painted a neutral gray. Four different types of goal boxes, two of each type, were constructed: they were (*a*) a black box with high hurdles, (*b*) a black box with low hurdles, (*c*) a white box with high hurdles, and (*d*) a white box with low hurdles. The hurdles were ¼-in. plywood painted the same color as a given goal box. Four of these hurdles were placed at equal distances throughout the length of a goal box. The high hurdles were 1½ in. high and the low ones ¼ in. high. Any given pair of these goal boxes could be presented on a given trial.

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Procedure

Two weeks prior to the experiment the *S*s were placed on a hunger schedule of 2 hr. of free feeding followed by 22 hr. of deprivation. This schedule was maintained throughout the experiment. During this initial period they were tamed by daily handling. They were then adapted to the apparatus by being placed successively in each of the four types of goal box and being left until they ate some of the wet mash placed in and about the food tray. On each of the following two days they were given eight forced runs from the starting box equally distributed between the two spatial positions and the four types of goal box.

The *S*s were then distributed into six groups, with an equal number of males and females in each. The groups were as follows:

Black-white reversal constant (*BWRC*). These *S*s learned eight discriminations with one brightness cue positive on the odd-numbered discriminations and the other brightness cue positive on the even-numbered ones. Half the *S*s in this group always had high hurdles in both goal boxes on every trial, and half had low hurdles.

High-low hurdle reversal constant (*HRC*). These *S*s similarly learned eight discriminations with one hurdle cue positive on the odd-numbered discriminations and the other on the even-numbered ones. For half the *S*s both goal boxes were white on every trial, and for half they were black.

Black-white reversal random (*BWRR*). These *S*s were treated exactly the same as the BWRC group except that the goal boxes differed not only in brightness and spatial position, but in that one always contained high hurdles and the other low hurdles on a given trial. These three dimensions were combined randomly on a given trial with the restrictions that (*a*) no pair of cues, such as black and left, would occur together for more than two successive trials, (*b*) the reward would not occur with either hurdle cue or either spatial position for more than two successive trials, and (*c*) all combinations of cues would occur equally often. Thus this group had one more random stimulus dimension present than did the BWRC group.

High-low hurdle reversal random (*HRR*). This group was treated exactly the same as the BWRR group except that the reward was correlated with one hurdle cue on the odd discriminations and the other on the even ones.

Change of dimensions (*CD*). These *S*s had the same stimulus arrangement as did the previous two groups. On the first discrimination the reward was correlated with one of the brightness cues, e.g., black. When this discrimination was learned, the reward was then correlated with one of the hurdle cues, e.g., high hurdles. On the third discrimination the reward again was correlated with black, the same brightness cue that had been positive on the first discrimination. This shifting from dimension to dimension, with the same cues always positive on a given dimension, was continued for 16 discriminations.

Change of dimensions and reversal (*CDR*). This group was treated exactly the same as the CD group on the first 2 discriminations. On the third, however, when the *S*s returned to the brightness discrimination, the reward was correlated with the white, the negative cue of the first discrimination. Similarly on the fourth discrimination when they returned to the hurdles dimension, the reward was correlated with the low hurdles, the negative cue of the second discrimination. This procedure was continued throughout 16 discriminations.

Originally six *S*s were assigned to each of the reversal groups and 12 to each of the change of dimensions groups. Due to the rigors of the motivation schedule and to middle ear infection, complete records were obtained for only five animals in each of the four reversal groups, ten animals in the CD group, and six in the CDR group. All training was by a Lashley-type correction technique so that a trial consisted of one rewarded response. Five trials a day, six days a week, were given with a half-hour between trials. The criterion of learning was 13 correct out of 15 consecutive trials.

RESULTS

The comparison of the CD and the CDR groups is shown in Figure 1, where the mean number of trials required to reach the criterion on each of the 16 successive discriminations is plotted for each group. It is apparent that starting with the third discrimination, the first one on which the two groups were trained differently, the CDR group learns each discrimination more slowly on the average than does the CD group. These differences were tested by assigning each *S* two scores, the sum of the trials required to reach the criterion on the last 7 black-white discriminations and the sum of the trials for the last 7 hurdle discriminations. When the mean differences between the CD and CDR groups for these two types of scores were tested, the resulting *t* values were significant beyond the .01 level in each case. This supports the suggestion that learning a new discrimination involving a different set of cues in a constant stimulus situation fails to break down a previously learned discrimination involving a different set of cues in that same situation.

The comparison of the four reversal groups in terms of the mean number of trials required to reach the criterion on each of the 8 discriminations is shown in Figure 1. An analysis of variance was performed on the trials to criterion for the first discrimination. The difference between the two black-white reversal groups versus the two hurdle groups was significant beyond the .01 level, that between the two random versus the two constant groups was significant beyond the .05 level. Thus, even with these few *S*s there is evidence that from the beginning the addition of a second random stimulus dimension "masks" or makes more difficult a given discrimination. The fact that the interaction in the above analysis was significant at the .05 level suggests that this masking is greater when the black-white dimension is introduced into the hurdle discrimination as a random variable than when the converse is true.

The same analysis was performed on the 7 reversal discriminations, 2 through 8, by assigning each *S* a score which was the sum of its trials to criterion on these 7 discriminations. It was necessary to convert the scores to logarithms in order to produce homogeneity of variance. Again the difference between the black-white and hurdle groups and the difference between the random and constant discriminations were each significant beyond the .01 level. There was, however, no evidence of a significant interaction effect.

There is an interesting contrast between the HRR group and the CDR group. The latter had 16 discriminations during which it reversed the hurdle discrimination seven times just as did the HRR group in its 8 discriminations. The CDR *S*s had learned the first hurdle discrimination by the end of the second discrimination, the HRR *S*s by the end of the first. Consequently, each *S* in the former was given a score which was the total number of trials including criterion trials required to complete the remaining 14 discriminations, and each *S* in the latter was given a similar score for the remaining 7 discriminations. The HRR group averaged a total of 676.0 trials for these 7 discriminations while the CDR group averaged 618.5 for the 14 discriminations. While not statistically significant for these few animals, this difference suggests the possibility that the interpolated black-white discriminations facilitated the hurdle reversal to a greater extent than did continuous training directly on the hurdle reversals.

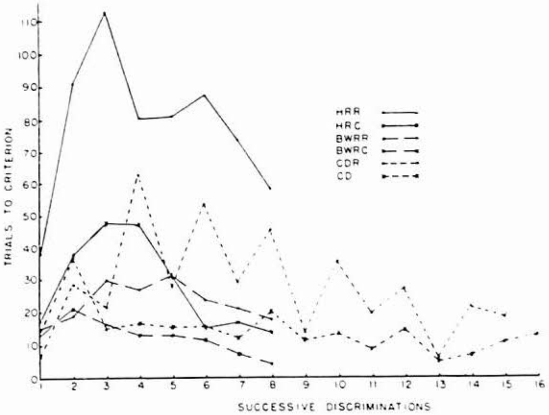

FIG. 1. Trials to criterion for each of the six groups on successive discriminations.

To obtain some suggestion as to the differences in systematic behavior between the various groups, the records were scored as follows. Any sequence of four or more trials on which the initial choice of an *S* was correlated with a given cue, e.g., four or more successive initial choices to the black, to the left, or to high hurdles, was classified as a run or systematic behavior. All shorter sequences were scored as unclassified trials. Thus, there were four scoring categories: runs correlated with the relevant dimension, with the irrelevant, with spatial position, or unclassified trials. The reason for choosing four trials as the minimum unit was that the trials were so arranged that no pair of cues, such as black and high hurdles, ever occurred together for more than two consecutive trials. Consequently, if an *S* tended to follow black for four consecutive trials, it would have done so despite the fact that black had been paired as a rule with all four of the possible combinations of space and hurdle cues. The runs counted were nonoverlapping in that a given

TABLE 1

Analysis of Systematic Behaviors Based on 8 Discriminations for Reversal Groups and 16 Discriminations for Change of Dimension Groups

Group		Category of Response			
		Irrelevant Dimension	Spatial Position	Relevant Dimension	Unclassified Trials
BWRR	Total trials	20.2	83.0	37.0	40.0
	Aver. run length	5.32	7.41	5.44	
	% of trials	11	46	21	22
BWC	Total trials		32.6	20.6	46.0
	Aver. run length		5.62	4.90	
	% of trials		33	21	46
HRR	Total trials	139.8	220.8	115.6	132.0
	Aver. run length	6.79	6.94	5.30	
	% of trials	23	36	19	22
HRC	Total trials		73.6	63.2	87.8
	Aver. run length		6.46	5.64	
	% of trials		33	28	39
CD	Total trials	99.8	31.8	42.8	48.0
	Aver. run length	6.68	5.01	4.84	
	% of trials	45	14	19	22
CDR	Total trials	189.5	92.7	54.8	105.7
	Aver. run length	6.98	5.62	4.57	
	% of trials	43	21	12	24

trial was assigned to only one of the four possible scoring categories. Each trial could be assigned unambiguously. Criterion trials were not included.

To obtain an approximate value for the expected percentage of trials that would be classified as systematic runs of this type if *S*'s behavior were purely random, empirical samples were constructed as follows. Using a set of 30 consecutive trials that had occurred in the experiment and a table of random numbers, it was determined which of the two goal boxes an *S* would have chosen on a given trial. Thirty-six such sets of trials were sampled. These were then scored for the four categories of response just as in the actual experiment. For the situation in which three stimulus dimensions were present, the percentage of trials was classified under each of the four categories as follows: position, 21.3; brightness, 17.3; hurdles, 24.5; and unclassified, 36.9. By chance, then, one would expect approximately 37 per cent of the trials to be unclassified and 21 per cent to be systematic responses in each of the other three categories. These percentages tend to be independent of the number of trials considered. Doubling the number of trials from 30 to 60 would add a negligible increment to the percentage of systematic behaviors because of the fact that occasionally a sequence of four might start at the end of the first set of 30 trials and continue into the second set of 30 trials. When these same data were scored as though only two stimulus dimensions were present, e.g., brightness and position, 54 per cent of the trials were unclassified and 23 per cent were systematic runs on each of the two dimensions.

The actual results of this type of analysis for the six groups are shown in Table 1. The scores presented are the average number of trials per animal of each type of response for the entire training period, i.e., 8 discriminations for the reversal groups and 16 for the change of dimension groups. It should be noted that in the four groups having two irrelevant stimulus dimensions, the BWRR, HRR, CD, and CDR groups, more than 75 per cent of their trials consisted of systematic runs of four or more trials in length. Several such runs tended to occur on each discrimination. The percentage of trials accounted for by this systematic behavior for the various groups appears to be independent of the total number of trials involved.

Comparing the four reversal groups, it is apparent that in going from the constant to the random conditions all means for the various categories tend to be increased. The increase in position responses, however, is disproportionate to the increase in other types of behavior, suggesting that when an additional irrelevant stimulus dimension is added, the additional number of trials required to master a discrimination consists largely of systematic position responses. An analysis of variance of the data for the reversal groups, using only the position, relevant, and unclassified categories for the random groups because they are the only ones held in common with the constant groups, is shown in Table 2. The important contrast is the interaction between random vs. constant reversal groups and the position vs. other types of response. This interaction is significant at the .02 level. This disproportionate increase in position responses with the introduction of a random irrelevant dimension occurs equally in the BWRR and the HRR group. Along with this tendency toward disproportionately increased position runs, there is also an increase in the number of systematic runs on the irrelevant dimension. This latter tendency is stronger in the HRR than in the BWRR group, presumably because of the greater "masking" power of the black-white as contrasted with the hurdles.

A similar result is found in the contrast of the types of systematic behavior shown by the CDR and the HRR groups, as indicated in Table 3. In this analysis all 16 discriminations for the CDR group were used. The difference in means for the two groups on systematic runs to the relevant and irrelevant dimensions shown in Table 1 is largely an artifact of the scoring. In the HRR group the negative stimulus of the present discrimination was always the positive stimulus of the immediately preceding discrimination. Consequently, when a discrimination was suddenly reversed and an *S* continued to respond systematically to the previously positive stimulus, it was counted as a run on the relevant dimension. In the case of the CDR group such a run to the previously positive stimulus was classified under the irrelevant dimension because of the change in dimensions involved from one discrimination to the next.

The important contrast is the interaction between the CDR vs. HRR group and the position vs. other types of response. This is significant at the .02 level even for these few animals. The suggestion is that the seven reversals of the hurdle discrimination in the CDR group are easier because the interpolated black-white discrimination prevents the building-up of systematic position responses such as are found in the HRR group.

The final analysis of the data concerned the differential decrease in these various types of behavior as discrimination training continued. For each animal in the four reversal groups the average number of trials per discrimination for each category of response on the first two reversals, discriminations 2 and 3, and the last two reversals, discriminations 7 and 8, was computed. The differences between these averages are shown in Table 4. For compari-

TABLE 2

Analysis of Variance of Position, Relevant, and Unclassified Responses During Eight Discriminations for the Four Reversal Groups

Contrast	*df*	Variance
1. Random vs. constant	1	38,658.82*
2. Black-white vs. hurdles	1	78,409.35**
3. Type of response		
a. Relev. vs. unclass.	1	3,010.23
b. Pos. vs. rel. & unclass.	1	16,077.67*
4. Interactions		
a. 1 × 2	1	13,953.75
b. 3a × 1	1	585.23
c. 3b × 1	1	17,304.00*
d. 3a × 2	1	1,050.63
e. 3b × 2	1	1,241.67
f. 1 × 2 × 3	2	1,264.55
5. Individuals	16	5,455.15
6. Ind. × Type of Response	32	2,469.46

* Significant at the .05 level.
** Significant at the .01 level.

TABLE 3

Analysis of Variance of Types of Response for the HRR and CDR Groups Based on 8 Discriminations for the HRR Group and 16 Discriminations for the CDR

Contrast	*df*	Variance
1. Type of response		
a. Irrel. vs. rel.	1	39,229.17**
b. Uncl. vs. irr. & rel.	1	364.00
c. Pos. vs. rel. & irr. & unclass.	1	6,736.72
2. HRR vs. CDR	1	18,682.69
3. Interactions		
a. 1a × 2	1	16,640.30
b. 1b × 2	1	786.62
c. 1c × 2	1	27,365.68*
4. Individuals	9	4,309.39
5. Ind. × Type Response	27	4,896.49

* Significant at the .05 level.
** Significant at the .01 level.

TABLE 4

Average Decrease in Trials for Various Types of Response Between First and Seventh Reversal of a Discrimination

Group	Type of Response			
	Irrelevant Dimension	Spatial Position	Relevant Dimension	Unclassified Trials
BWRR	−0.6	4.5	2.9	−0.7
BWC		3.1	4.7	5.2
HRR	7.8	19.2	5.1	5.5
HRC		13.2	8.7	5.2
CD	3.8	1.9	0.9	0.8
CDR	4.0	11.0	3.6	2.7

son similar averages were computed for the CD and CDR groups involving discriminations 3, 4, 5, and 6 and discriminations 13, 14, 15, and 16, even though no reversals were involved in the CD group. It is apparent from this table that three out of the four reversal groups show the maximum reduction in trials to the criterion as a result of a decrease in systematic responding to the position cues. The exception is the BWC group. In the change of dimensions groups, it is also a decrease in systematic response to either the position or to the irrelevant dimension that accounts for most of the observed decrease in trials.

DISCUSSION

The results of this study must be interpreted with caution, first, because of the relatively few *S*s in each group, and, second, because the statistical properties of the measure used to indicate systematic behavior are largely unknown.

One of the more suggestive results of the experiment is the contrast between the CD and the CDR groups. It is quite clear that reversing the positive and negative cues each time an *S* returns to a given dimension, as in the CDR group, produces increased interference as contrasted with the performance of the CD group, where a reversal is not involved. There are at least two possible interpretations of this effect. It is possible that when the CD *S*s learn the hurdle discrimination and then are shifted to the black-white, the time they spend on the black-white is insufficient to equalize the habit strengths of the two cues on the hurdle dimension. This would mean that even though their performance on the black-white reached criterion accuracy, there was still a latent discrimination on the hurdles. Consequently, when these *S*s returned to the hurdle discrimination, with no changes in the positive and negative cues on this dimension, they would show positive transfer. The CDR group on the other hand would show negative transfer. The crucial test of this hypothesis would be to train additional groups on these two types of discrimination but with varying amounts of overlearning on each. In terms of the continuity viewpoint, this should equalize any residual discrimination, and thus remove the difference between the CD and CDR groups. Such a study is underway at present.

If it is assumed that this overlearning does not get rid of the superiority of the CD group, it would support an interpretation that during the interpolated black-white discrimination the hurdle discrimination is largely nonfunctional in the sense that the response tendencies associated with these cues remain unchanged even though the *S*s are being reinforced and nonreinforced in the presence of these cues.

Another surprising finding, though a tentative one, is the contrast between the HRR and the CDR groups. The CDR group actually learned eight black-white reversals and eight hurdle reversals in somewhat fewer trials than it took the HRR group to learn just eight hurdle reversals. This superiority of the CDR group becomes difficult to explain when it is realized that for these *S*s the positive and negative cues of the previous hurdle discrimination were each receiving partial reinforcement during the interpolated black-white discrimination. Consequently, it would be expected that these interpolated trials would have less influence in erasing the hurdle discrimination than would the same number of trials for the HRR group, where the previously positive cue is being consistently nonrewarded and the previously negative cue is being consistently rewarded as the result of the correction method used.

One possible basis for the above finding is suggested by Tables 1 and 3. There it is shown that the CDR group not only shows a greater absolute number of systematic runs to position than does the CD group, but that this type of response forms a disproportionately larger percentage of all systematic behaviors in the CDR than in the CD group. The suggestion is that the reversal of a discrimination, in contrast to a nonreversal, results in the *S*'s showing more frequent sequences of runs to irrelevant aspects of the stimulus situation. If it is assumed that during these runs the *S* learns relatively little about the relevant cues in the discrimination, even though *S* is being consistently rewarded and nonrewarded on them, this would account in part for the greater difficulty of the CDR as compared to the CD problems.

Such a tendency, i.e., to "displace" or

respond to new aspects of the stimulus situation when a familiar reinforcement schedule is suddenly interrupted as in a reversal, also would suggest one reason for the fact that the CDR group reversed seven hurdle discriminations and seven black-white discriminations in somewhat fewer total trials than required by the HRR group to reverse just seven hurdle discriminations. If upon the reversal of a discrimination *S*s tend to begin responding systematically to other aspects of the stimulus situation, this would be a pure loss to the HRR group, where hurdles are always the relevant cue. It, however, would facilitate the learning of the CDR group on occasion. When the correlation between the reward on a given cue, e.g., hurdles, is changed for this group, the experimental procedure requires that these animals begin responding to a different aspect of the stimulus situation, e.g., brightness. Thus a tendency to "displace" might speed up the learning of the new problem.

This possibility also offers a tentative explanation of why the introduction of additional irrelevant dimensions into a discrimination reversal situation results in a disproportionate increase in the systematic runs to position. The greater the number of irrelevant stimulus aspects in the situation, the greater the likelihood that systematic runs will develop and persist on aspects that contribute little to the learning of the reversal.

There remains the possibility that a part of the progressive improvement shown during successive discrimination reversals can be accounted for in terms of a decrease in the tendency to respond systematically to irrelevant aspects of the situation. While the evidence from the present experiment is only suggestive in this respect, the data in Table 4 would seem to indicate that the reduction in position responses accounts for a considerable part of the improvement shown in three of the reversal groups.

SUMMARY

Six groups of animals were trained on a simultaneous discrimination apparatus. Four of the groups had three stimulus dimensions randomly combined on successive trials; these were brightness differences, hurdle differences, and spatial differences. In this situation one group, HRR, learned 8 brightness reversals, and a second group, BWRR, learned 8 hurdle reversals. The third group, CD, had 16 discriminations involving a "change in dimensions," e.g., the first discrimination had black positive, the second high hurdles positive, the third black positive, the fourth high hurdles positive, and so on. The fourth group, CDR, had 16 discriminations involving both change of dimensions and reversal, e.g., the first had black positive, the second high hurdles positive, the third white positive, the fourth low hurdles positive, and so on. The fifth group, BWC, had a discrimination situation involving only two stimulus dimensions, brightness differences and spatial differences, and learned 8 brightness reversals. The sixth group, HRC, also had two stimulus dimensions, hurdle differences and spatial differences, and learned 8 hurdle reversals.

1. It was shown that the CD group learned significantly more rapidly than did the CDR group. This was interpreted as possible support for the view that when two stimulus dimensions are present in a given situation, one may remain essentially nonfunctional while the animal is responding systematically to the other.

2. The rate of reversal was significantly faster in the groups having only two stimulus dimensions than in the groups having three.

3. The CDR group completed 16 discriminations, including 8 hurdle reversals, more rapidly than the HRR group completed 8 hurdle reversals alone.

4. The slower learning of the reversal groups with three dimensions was shown to be accompanied by a disproportionate increase in systematic behavior on the position dimension.

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SUCCESSIVE ACQUISITIONS AND EXTINCTIONS OF A JUMPING HABIT IN RELATION TO SCHEDULE OF REINFORCEMENT

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Studies in which a conditioned response has been repeatedly conditioned and extinguished have uniformly shown marked, progressive increases in rate of both conditioning and extinction (1, 2, 8, 9); these studies have, however, been conducted with massed trials, and, as pointed out by previous writers (2, 9), it is likely that the changes in rate simply reflect formation of a discrimination with the stimulating aftereffects of reinforced and nonreinforced trials serving as positive and negative cues, respectively, for responding on subsequent trials. It is our purpose in this experiment to determine what characteristics, if any, of simple instrumental learning exhibit progressive changes over repeated conditioning and extinction series when controls have been instituted for a discrimination based on reinforcement and nonreinforcement.

The most obvious control procedure is to space the trials and remove the animal from the apparatus between trials so that stimulus aftereffects of one trial cannot serve as discriminative cues for the next. A second possibility is to utilize random reinforcement during the conditioning series, thus markedly attenuating the over-all correlation between stimulus aftereffects of one trial and condition of reinforcement on the next. We have adopted both measures in the present study, arriving at the design summarized in Table 1. Two groups of rats were subjected to repeated conditioning and extinction of a jumping habit with relatively spaced trials; alternate acquisition series were carried out under continuous reinforcement and random reinforcement. The principal observations that will interest us are (*a*) changes in rate of conditioning from earlier to later acquisition series under the same condition of reinforcement; (*b*) changes in rate of extinction from earlier to later extinction series following the same condition of reinforcement; and (*c*) differential effects of continuous as compared with random reinforcement.

Since the procedure of partial reinforcement differs from that of repeated conditioning and extinction only in the particular manner of grouping reinforced and nonreinforced trials, it seems reasonable to expect that once the complicating factors associated with massed trials have been eliminated, the two cases should be subject to a common theoretical interpretation. Consequently, it will be of interest to see whether or not a contiguity-interference theory which has been worked out in connection with recent studies of partial reinforcement (10) will handle the data of this experiment. It will also be possible to obtain evidence relative to a number of predictions from statistical learning theory (4) having to do with day-to-day regression during conditioning and recovery during extinction.

METHOD

Subjects and Apparatus

The *S*s were 15 male hooded rats from the colony maintained by the Indiana University department of psychology; they were approximately 275 days old at the beginning of the main experiment.

A Lashley-type jumping stand was modified to meet the requirements of the experiment. The jumping platform was constructed of ¾-in. plywood, 7½ in. wide by 10 in. deep, and was located 8¾ in. from the windows; the edge of the platform was 2 in. higher than the bottom of the windows. The windows were 6 in. high, 5⅝ in. wide, and ½ in. apart. The feeding platform was divided, by means of a sheet metal partition 10 in. high, into two 12-in. by 19½-in. compartments, one accessible from each window. The jumping platform and the panel facing it were painted flat black and enclosed with black cloth screening. Two 6-w. bulbs mounted under the platform provided continuous illumination. The feeding platform was painted white and illuminated by a 25-w. bulb centered overhead. The doors used during pretraining were made of manila cardboard, hinged at the top. The doors used during the main experiment were made of .020-in. aluminum, again hinged at the top; one had the top half black and the bottom half white, and the other had the top half white and the bottom half black. The positions of the doors were never exchanged.

Procedure

Throughout the experiment the rats were maintained on a 23-hr. feeding schedule. During preliminary training the entire daily ration was given on the feeding platform of the jumping stand. During the main experiment the rats were fed the balance of their daily ration in their home cages 5 to 10 min. after the experimental period. The food used throughout was a mash made from ground Purina Laboratory Chow, with quantity adjusted to maintain approximately constant weight. Water was available in the home cages.

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[1] Participation of the second author was facilitated by his tenure as S. S. R. C. faculty research fellow.

Preliminary training. Throughout preliminary training both doors were unlocked and jumps to either side were reinforced with food. At first the jumping platform was moved up so the rats could walk through the windows; next, the rats jumped through the open windows and, finally, through the cardboard doors. This training was carefully graduated so that the rats were never punished by a fall into the net. After the rats had learned to jump, they were given 62 days of training designed to eliminate position preferences. Each day each rat was given two free trials and then a series of hand-guided trials interspersed with free trials until it had jumped at least twice through each window on free trials.

It should be noted in passing that one purpose of this extensive pretraining was to determine whether or not the results of Zeaman and House (11) concerning alternation following forced trials in the T maze could be reproduced in the jumping situation. The answer is that they could not. The rats never manifested any significant tendency to alternate sides following guided trials. Furthermore, during the main experiment which followed, both doors were unlatched on *all* trials, and 14 of the 15 rats went through the entire experiment, approximately 300 free-choice trials, without ever deviating from their initial position preferences; the remaining rat made 59 consecutive responses to the right and then shifted "spontaneously" to the left side for all the remaining trials.

Main experiment. Except for the operations of reinforcement and nonreinforcement, all trials of the main experiment were run under the same conditions. Both doors were always unlocked, and dishes of mash were always in place at the rear end of the feeding compartments; on nonreinforced trials sheet metal barriers were inserted in front of the food dishes. At the beginning of a trial, one of the *E*s placed the rat on the jumping platform facing away from the windows. The second *E* timed with a stop watch the interval from the release of the rat until the opening of one of the doors; times were recorded to the nearest half second. Following a jump the rat remained on the feeding platform for 10 sec., then was put back in its home cage. Each rat was run four trials each day during both conditioning and extinction series. The three rats in a cage were run in rotation so that the intertrial interval within daily blocks varied from 2 to 4 min. throughout the experiment except for occasional extinction trials when jumping times as long as 10 min. occurred.

The number of days of training per series indicated in Table 1 applies strictly to ten rats, six in group I and four in group II, that started the main experiment first and ran contemporaneously throughout. Five additional rats, two in group I and three in group II, were first given seven days of extinction, for reasons that are not germane to the present report, and then started on the first conditioning series. Owing to scheduling difficulties the latter five rats received 12, 12, and 13 days of training in the three conditioning series. In the presentation of results the data from the two batches of animals have been combined since each animal serves as its own control in all the main comparisons and since all the trends reported hold for all subgroups.

TABLE 1

Experimental Design: Number of Days Under Each Procedure

Group	N	Series 1		Series 2		Series 3		Series 4
		Acq.	Ext.	Acq.	Ext.	Acq.	Ext.	Acq.
I	8	14 100%	8	14 50%	8	14 100%	8	7 50%
II	7	14 50%	8	14 100%	8	14 50%	8	7 100%

RESULTS

For purposes of later discussion, it will be helpful to consider the results in two categories: (*a*) those related to successive series, and (*b*) those attributable to the schedule of reinforcement.

All results will be reported in terms of reciprocal latency, generally referred to for brevity as *response speed.* Statistical tests are based upon two-way analyses of variance modified in accordance with Kogan's suggestion (7) to allow for correlation among repeated measures. In each case, group differences are tested against the variance estimate from rats-within-groups while differences among series means and groups by series interaction are tested against the variance estimate from rats-within-groups by series interaction. It will be clear from Table 1 that differential effects of 100 per cent and 50 per cent reinforcement will show up as significant groups by series interactions.

Series Effects

In general, both learning rates and terminal levels increased from series to series. Within the various series, curves of mean response speed vs. days were negatively accelerated and appeared to have reached asymptotes in each of the first three series. Differences between the last two daily means were small and insignificant for both groups in the first three acquisitions; considering the individual changes, there were 22 increases, 22 decreases, and 1 case of no difference. Mean response speed over the last two days has been taken

TABLE 2

Mean Reciprocal Latencies over Last Two Days of Acquisition

Means

Group	Series		
	1	2	3
I	.334	.294	.486
II	.104	.286	.242

Analysis

Source of Variance	F	p
Groups	4.49	<.05
Series	7.94	<.01
Groups × Series	6.72	<.01

TABLE 3

Increase in Mean Reciprocal Latency from Last Day of Extinction to First Day of Reacquisition

Means

Group	Series		
	2	3	4
I	.058	.210	.202
II	.068	.149	.161

Analysis

Source of Variance	F	p
Groups	<1.0	
Series	9.73	<.01
Groups × Series	<1.0	

TABLE 4

Decrement in Response Speed from Last Trial of One Acquisition Day to First Trial of the Next

Means

Group	Series		
	1	2	3
I	.012	.030	.085
II	.045	.124	.069

Analysis

Source of Variance	F	p
Series	4.31	<.05
Groups	1.36	>.05
Groups × Series	4.19	<.05
Grand mean	49.56	<.001

as an estimate of asymptotic level for each group in each of the first three acquisitions, and these values are included in Table 2. The over-all increase in mean terminal response speed from series to series is significant at the .01 level. The pattern of differences is unchanged if only the first trials of daily blocks are considered.

As one measure of learning rate, we have taken the increment in mean response speed from the last day of each extinction to the first day of reacquisition; these values are given in Table 3. It will be seen that these increments increased from series to series for both 100 per cent and 50 per cent conditions. This effect is significant at the .01 level.

As a second measure of learning rate, we have computed for each reacquisition the increment in mean response speed from the first trial of the first day to the first trial of the second day. An analysis of variance for series 2, 3, and 4 indicated no significant differences. Since, however, the F for series barely failed to reach the .05 level, t tests were computed for series 2 vs. series 4, a comparison in which the same rats appeared under the same conditions of reinforcement. For the 100 per cent groups the t value was 6.24 with 6 df, indicating an increase in learning rate significant at the .001 level. The corresponding increase for the 50 per cent group was not significant.

Throughout all acquisition series there was a tendency for some regression in response speed from the last trial of one day to the first trial of the next. This effect is significant at the .001 level as shown in Table 4.

Extinction curves were negatively accelerated and appeared to reach asymptotes in each series. Differences in mean response speed between the last two days of each extinction series were small and insignificant; of the 45 individual changes, 20 were increases, 22 decreases, and 3 were constant. Mean response speeds over the last two days have been taken as estimates of asymptotic level for each series, and these values are included in Table 5. Mean terminal response speed increased significantly (.02 level) from series to series regardless of the preceding reinforcement schedule. Initial decrement during extinction, as measured by differences in mean response speed between the last day of each acquisition series and the first day of the following extinction series, did not change significantly from series to series. Extinction curves plotted in terms of first trials of daily blocks exhibit progressive reductions in slope from series to series. Considering the differences in mean response speed between the initial trials of the first and second days of extinctions 1 and 3, both the 100 per cent and 50 per cent groups show decreases, the former just failing to reach significance at the .05 level (t of 2.08 with 7 df) and the latter being insignificant. In relative terms, the changes are more striking in both cases. Expressing response speed on the first trial of day 2 as a proportion of response speed on the first trial of day 1, we obtain mean values of .420 and .610 for the 100 per cent and 50 per cent groups, respectively, on extinction 1, which rise to .746 and .768, respectively, on extinction 3; the increase is significant at the .05 level by a sign test for the combined groups (p = .035 for a two-tailed test), and for the 100 per cent group alone (p = .04 for a two-tailed test), but not for the 50 per cent group alone.

Partial vs. Continuous Reinforcement

In the acquisition series, asymptotic levels under 100 per cent reinforcement were significantly higher than those under 50 per cent reinforcement (.01 level). In the extinction series, however, the terminal level exhibited no significant effect of preceding reinforcement schedule. The analyses are summarized in Tables 2 and 5, respectively.

The 50 per cent and 100 per cent groups did not differ significantly with respect to either of the measures of learning rate described above. In extinction, however, initial decrements were significantly greater (.01 level) following the 100 per cent series than following the 50 per cent series, as indicated in Table 6.

The detailed course of extinction was quite different following 100 per cent as compared with 50 per cent reinforcement. In Figure 1 we have plotted pooled mean curves for extinction following the two conditions. It may be seen that following 100 per cent reinforcement, response speed declined within daily blocks and recovered between blocks, while following 50 per cent reinforcement, response speed declined between daily blocks and recovered within blocks. In the former case there was a large mean decrease in response speed from the first to the second trial of a daily block, while in the latter case there was an increase, the difference being significant at the .001 level. In the 100 per cent case the spontaneous recovery, measured in terms of the increase in mean response speed from the last trial of one block to the first trial of the next, was large and significant (.001 level) following the first day, but decreased rapidly on successive days and was insignificant after the second; in the 50 per cent case the corresponding difference was uniformly in the opposite direction, but the over-all mean decrease was small and did not yield a significant t value.

TABLE 5

Mean Reciprocal Latencies over Last Two Days of Extinction

Means

Group	Series 1	Series 2	Series 3
I	.062	.092	.121
II	.044	.052	.079

Analysis

Source of Variance	F	p
Groups	1.52	>.05
Series	5.47	<.02
Groups × Series	<1.0	

TABLE 6

Decrease in Mean Reciprocal Latency from Last Day of Acquisition to First Day of Extinction

Means

Group	Series 1	Series 2	Series 3
I	.177	.089	.262
II	.042	.145	.018

Analysis

Source of Variance	F	p
Groups	10.41	<.01
Series	<1.0	
Groups × Series	8.17	<.01

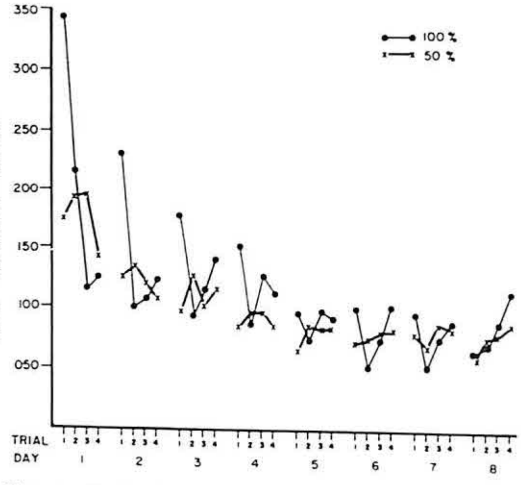

FIG. 1. Extinction following 100 per cent as compared with 50 per cent reinforcement. The curves represent means over *S*s and series.

DISCUSSION

It appears that when artifacts associated with massed trials have been eliminated from a simple instrumental learning situation, the result of repeated conditioning and extinction is a progressive increase in the effectiveness of reinforcement and a progressive decrease in the effectiveness of nonreinforcement. This finding lends support to the view that repeated conditioning and extinction is simply a special case of partial reinforcement and should be handled by the same theory.

In an extensive investigation of runway behavior under partial reinforcement, Weinstock (10) found an inverse relationship between resistance to extinction and percentage of reinforcement even under conditions of 24-hr. trial spacing. He pointed out that this result might be accounted for if the following specific assumptions were added to standard contiguity-interference theory (3, 6): (*a*) After continuous reinforcement, the occurrence of nonreinforcement evokes varied locomotor behavior which becomes conditioned to cues that formerly evoked the running response and in turn leads to increased running time; (*b*) on nonreinforced trials, these varied reactions to nonreinforcement tend to extinguish ("habituate") so that after a lengthy partial series, a nonreinforced trial evokes few responses that actively compete with the running response.

In the present study, similar considerations would apparently account rather directly for the greater initial extinction decrement following continuous as compared with partial reinforcement, for the progressive slowing down of extinction from series to series, and for the large increases in rate of acquisition under partial reinforcement. Formal evaluation of this interpretation must await a more detailed explication of the contiguity model as applied to this type of learning situation.

The progressive increase in slopes and apparent asymptotes of acquisition curves under continuous reinforcement was not predicted a priori. On the basis of observations made during the experiment, it seems likely that this effect may be attributable, at least in part, to the gradual dropping out of "unnecessary" components of the jumping response. On early acquisition trials some of the responses that occur on the starting platform prior to jumping become strongly conditioned, so that the animal persists in going through what looks like a routine or "ritual" on each trial. These extra responses will not extinguish, according to a contiguity interpretation, unless they happen to fail on some trial; and this failure may not take place until during extinction the varied responses evoked by nonreinforcement displace some of the strongly established "unnecessary" responses.

In statistical learning theory (3, 4, 5) it is assumed that a repetitive experimental situation determines a population of stimulus elements from which a random sample is available during any one experimental period. Even though the reinforced response becomes conditioned to all the available elements during an acquisition period, only a portion of these elements will appear in the sample that is available during the next period, together with other stimulus elements, some of which may not have been previously conditioned to the response. Consequently it is predicted (4) that during acquisition there will be a regression in response probability, and therefore response speed (3), from the last trial of one period to the first trial of the next, with the magnitude of this regressive effect decreasing exponentially during the series. These effects are expected under both 100 per cent and 50 per cent reinforcement schedules, but to a smaller extent in the latter case since fewer of the elements present during a period would become conditioned. The acquisition data exhibit the predicted regressive effect under both conditions; the magnitude of the effect decreases, although not significantly, over the series, and is somewhat smaller, although not significantly so, for the 50 per cent condition.

Similar period-to-period fluctuations in the stimulus sample should occur during extinction, resulting in spontaneous recovery of response speed from one period to the next. The amount of recovery should be initially large, at least for the 100 per cent group, and should decrease exponentially as the series progresses. It can be seen in Figure 1 that the predictions are nicely borne out for the 100 per cent group; the recovery effect is significant at the .01 level following the first extinction period, then drops to insignificance for the remainder of the series. Following 50 per cent reinforcement there is no response decrement within periods and consequently no possibility of spontaneous recovery.

SUMMARY

Rates of learning were studied during successive acquisitions and extinctions of a jumping habit. Two groups of rats were given four acquisition series, alternately under continuous and partial reinforcement, interspersed with three extinction series. Each series comprised a sequence of daily trial blocks with relatively spaced trials within blocks. It was considered that the procedure effectively precluded the type of discrimination based on stimulating aftereffects of reinforcement and nonreinforcement which may have been responsible for the progressive changes in learning rate found in previous studies under massed trials. Results were that:

1. Learning rates and asymptotes increased progressively with successive acquisitions under both conditions of reinforcement.

2. Successive extinctions yielded progressively shallower curves and higher terminal levels of response speed.

3. Mean terminal response speeds were higher under continuous than under partial reinforcement.

4. Extinction rates were similar following continuous and partial reinforcement except for a greater decrement on the first extinction day following continuous reinforcement.

5. In all acquisition series there was a tendency for some regression in response speed from the last trial of one block to the first trial of the next.

6. Following continuous reinforcement, extinction occurred within daily blocks with recovery between blocks; following partial reinforcement, recovery occurred within daily blocks and decrement between blocks.

The findings concerning day-to-day regression and recovery during acquisition and extinction, respectively, are in accordance with predictions from statistical learning theory. The other findings suggest the nature of modifications in standard contiguity-interference theory which may permit a unified interpretation of both the partial reinforcement and the repeated conditioning-extinction procedures.

A subsidiary result, obtained during preliminary training on the jumping stand, was that in this situation blocks of massed, forced trials do not lead to alternation on test trials.

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THE FACILITATION OF EXPERIMENTAL EXTINCTION BY RESPONSE PREVENTION AS A FUNCTION OF THE ACQUISITION OF A NEW RESPONSE

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In a previous experiment which verified and extended Hull's frustration hypothesis (1), Page and Hall (3) demonstrated that the blocking of avoidance responses led to a more rapid cessation of the response than would be achieved through traditional extinction procedures. In an attempt to extend and further verify Hull's frustration hypothesis, two groups of albino rats were trained to escape from an electrically charged grid. In the first five extinction trials of the experimental animals, a door leading from the avoidance chamber remained closed, making escape impossible. A comparison of the total number of trials to extinction revealed that the blocked animals extinguished at a significantly more rapid rate than those animals that were permitted access to the escape chamber throughout the extinction procedure.

In discussing these results two somewhat different explanations were offered to account for the "advantage" demonstrated by the "blocked" group. It was suggested that any response which was associated, in an appropriate temporal sense, with the absence of shock, would be reinforced by virtue of the earlier shock training. Animals that were prevented from leaving the avoidance chamber would be "rewarded" for remaining on the grid in that no shock was forthcoming during extinction. An alternative explanation dealt with the possibility that through a learning process neutral stimuli which had originally been associated with the painful electric stimulus were subsequently paired with its absence. The major differences in these explanations are that in the first it is posited that the avoidance chamber remains capable of eliciting fear but the organism has learned a response appropriate to its reduction. In the second explanation it is suggested that neutral stimuli have lost their capacity to arouse the drive.

The present study was conducted in the interest of determining which of these two explanations appears most feasible.

METHOD

Subjects and Apparatus

The *S*s were three groups of experimentally naive albino rats of the Sprague-Dawley strain. In each group there were ten male *S*s approximately 130 days old.

The apparatus consisted of two wooden boxes of identical dimensions. Each box measured 15 in. by 9 in. by 12 in. Three walls and the ceiling of the first box were solid and painted white while the remaining side was of plate glass to permit observation of *S*. The second chamber was similar to the first with the exception that black rather than white paint was used. The floor of the first chamber, the shock box, was a grid made of ⅛-in. brass welding rods placed at ½-in. intervals. The floor of the second box, the neutral chamber, was of a solid material painted black. The two boxes were placed end to end and connected by a vertically sliding door which was operated by *E*. Hinged covers on both boxes permitted placement of *S*s in the apparatus and their removal at the end of a trial.

The grid was connected to a "grid confusing" circuit which provided for a shock of approximately .3 ma. at 60 cycles, in a consistently changing pattern. When the current was turned on, *S* was shocked several times a second, as long as it remained on the grid and in contact with any two or more bars. Further details of this apparatus are presented elsewhere (6). The switching device which made a clearly audible clicking sound was turned on before the shock was delivered, as indicated in the procedure below.

Procedure

Learning Series

Experimental group I (not blocked). Each animal was permitted 1 min. in the apparatus with the door between the chambers remaining open and was then placed in a retaining cage. The first trial began 20 sec. later when *S* was placed in the shock box. The door between the chambers remained closed for 5 sec. and was then raised. Simultaneously, the shock box was provided with additional illumination and the switching device was set in operation. The light source consisted of a 15-w. lamp fixed in a box with a 1-in. square aperture which was placed against the viewing window of the chamber. Two seconds later, a total of 7 sec. after the animal had been placed in the box, the current was turned on, and the grid remained charged until the animal had moved through the door into the neutral chamber. The door was lowered and 10 sec. later the animal was removed and placed in the retaining cage. The second trial commenced 20 sec. later. This procedure was followed until *S* reached the criterion of three successive escapes in the 2-sec. interval between the opening of the door and the onset of the shock.

Experimental group II (blocked). The learning procedure for *S*s in this group was identical in every respect with that of animals in experimental group I.

Control group. These animals received no avoidance training.

Extinction Series

Experimental group I (not blocked). The extinction series was started 20 sec. after the last learning trial. The procedure was identical to that of the learning series with the exception of the absence of current in the grid. Trials were continued until the animal failed on three successive occasions to leave the shock box within 10 sec. after the door had been opened.

Experimental group II (blocked). For the first five extinction trials of the second experimental group, the door between the two chambers remained closed. The animal was retained in the shock box for 15 sec. and was then removed to the retaining cage. Visual cues provided by the light source and auditory stimuli attendant upon the operation of the switching device were dealt with in exactly the same manner as in the learning series. Beginning with the sixth trial, the door was raised, and the remaining trials were identical in all respects to those of animals in experimental group I.

Operant Learning Series

Experimental groups I, II, and controls. Approximately 24 hr. after the avoidance learning and extinction series (for animals in the experimental groups) operant trials were begun. Control *S*s had no avoidance training at the beginning of the operant procedure. The *S*s in all three groups were without food 24 hr. before this series commenced. Trials were conducted in blocks of five. The animals were placed in the second box, the neutral chamber for the avoidance training, and 5 sec. later the door between the boxes was raised, the shock box was illuminated, and the switching device was set in operation. A small pan, containing a fresh, moist mash of Purina Dog Chow had been placed in the middle of the grid floor of the shock chamber. After 5 min., if the animal had not moved into the shock box, the door was closed and *S* was removed from the apparatus and placed in the retaining cage to await the next trial 20 sec. later. If the animal moved into the shock chamber, it was allowed to remain there for 30 sec. (in which to eat) before being removed and placed in the retaining cage. After five trials, the animal was placed in its home cage where it remained for from 60 to 90 min. while three other *S*s were run through five similar trials each. At the end of this delay, each *S* experienced five more similar trials.

RESULTS

As demonstrated earlier, the blocking of responses early in the extinction trials results in more rapid extinction. Although experimental groups I and II did not differ significantly with respect to the number of trials necessary to reach the learning criterion, group II (blocked animals) required significantly fewer trials to reach the extinction criterion. The difference is significant at the .02 level of confidence.

TABLE 1

Number of Trials to Reach Learning and Extinction Criteria for Experimental Groups

Group	N	Learning		Extinction		t	p
		Mean	σ	Mean	σ^*		
I (normal)	10	7.40	4.91	30.00	21.65	3.13	.02
II (blocked)	10	8.50	7.39	7.60^t	6.36		

* The difference between the extinction variances is significant (t = 3.02). In line with the recommendations of Snedecor (4) the degrees of freedom were halved before they were entered in the t table.

Response latencies in the operant condition were treated as the dependent variable. Increased latencies were judged to indicate that stimuli associated with the shock chamber continued to elicit avoidance behavior.

All latencies, measured in seconds, were converted into $\log_{10}$ units. On operant trials on which *S* did not move into the shock box, latencies were scored as 300 sec. A mean was obtained for each *S*'s ten operant trials. A mean of the mean latencies for *S*s in each of the three groups was calculated and served as a basis for comparison. The results of this comparison appear in Table 2.

The results presented in Table 2 are rather clear-cut in indicating that all groups differed significantly from one another in the mean latencies observed. The control group showed the lowest latencies. Experimental group I (not blocked) was next, while experimental group II (blocked) showed the highest latencies with respect to returning to the shock chamber. All mean differences are significant beyond the .01 level of confidence. In all cases, differences between variances fall well short of significance.

When the first block of five trials is considered, Figure 1 reveals clear graphic differences between the three groups. In the second block of trials the disposition of the experimental groups remains constant while the latencies of control animals rise appreciably.

TABLE 2

Comparison of Experimental Group I and II and Control Group Latencies for the Operant Trials

Group	df	Mean Diff.	σMean Diff.	p
Exp. I & II	19	3.90	.200	.01
Exp. I & controls	19	3.20	.246	.01
Exp. II & controls	19	6.10	.217	.01

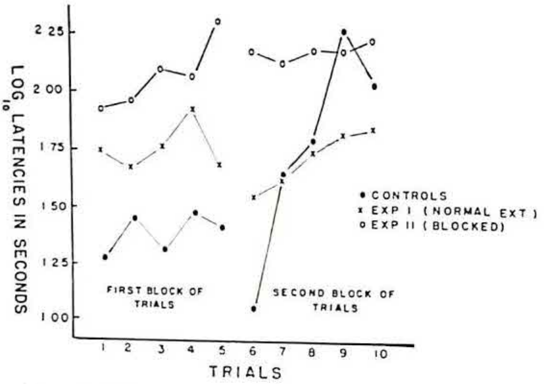

FIG. 1. Mean $\log_{10}$ latencies by trials for *S*s in experimental and control groups

DISCUSSION

The evidence provided by this experiment lends continued support to the notion that the interruption of avoidance responses facilitates the extinction of such behavior. These results confirm the earlier findings of Page and Hall (3) as well as the earlier experimentation of Williams and Williams (5) with an operant response. Both these earlier studies represented attempts to assess Hull's hypothesis that the "frustration" of goal-oriented responses led to a condition akin to experimental extinction (1).

In addition, the present investigation tends to clarify the process by which more rapid extinction occurs. Explanations of this finding had involved, on the one hand, diminished drive strength, while, on the other, it was suggested that a new response was acquired which competed with the running and escape. It would follow that if the first explanation were to hold, animals that had been blocked should not differ from those extinguished in a traditional fashion in their approach to the avoidance chamber when it served as a goal box (the operant condition). If stimuli that had acquired drive-producing properties were again rendered neutral, they would not be effective in eliciting avoidance reactions when *S* returns to the former shock chamber for food. However, if the more rapid extinction rate results from the effects of response competition, these stimuli would be considered to retain their drive characteristics which would be manifested in a situation where *S* returns to the avoidance chamber. The results of this study tend to support this second explanation in that those animals whose extinction followed the blocking of avoidance responses demonstrated a greater "reluctance," as measured by response latencies, to return to the avoidance chamber.

Finally, it should be noted that both experimental groups showed significantly longer latencies than control *S*s that had not had prior experience with the avoidance chamber. It appears that even when animals are extinguished in a traditional fashion, they still retain some aversion for the shock chamber when tested in this fashion. It should be pointed out that *S*s in experimental group I were placed in the operant condition one day after their avoidance training and extinction. Spontaneous recovery of the avoidance response may have been sufficient to account for latencies which exceeded those of the control group.

SUMMARY

This study was done in the interest of clarifying the process by which albino rats, prevented from making an avoidance response early in extinction trials, extinguish more rapidly than those treated in a traditional manner. It was demonstrated that when the avoidance chamber was treated as a goal box, latencies were significantly greater for animals whose avoidance responses had been interrupted early in the extinction of previous avoidance training than for a group that had been extinguished in a normal fashion and a control group of naive *S*s. These findings were interpreted to suggest that more rapid extinction following response interruption results from the acquisition of a new response which competes with running avoidance.

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PLACE AND RESPONSE LEARNING: LEARNING TO ALTERNATE

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In isolating "what is learned" one recent approach has been the study of differences in acquisition rates of particular perceptual-motor habits by the rat under conditions which make for "place" learning, and under "response" learning conditions (2, 5). It has been presumed that evidence exists for the "primacy" of spatial learning when an animal has demonstrated that a habit is acquired under spatial learning procedures (i.e., rich extramaze visual environment) more rapidly than when a similar habit is acquired under response learning procedures. A crucial test of exactly what is learned has not been forthcoming in any of these studies, since the experimental manipulations involve either a change in the environment, or else response tendencies are pitted against the environmental support.

As Blodgett and McCutchan (1) have suggested, the ideal case would be one in which it is possible for a spatial habit and/or a response habit to be acquired simultaneously, followed by a test to determine which has been acquired. In their experiment, however, the visual environment, which has been demonstrated as crucial to the development of a place habit (2), was highly restricted. An experiment to test their suggestion is described below.

METHOD

Fifteen male hooded rats (age 40 days) were placed on a 15-hr. food deprivation schedule for a period of three weeks. During this time they were handled each day at feeding time and allowed to roam at will on a large table top in the vivarium. This period of play and feeding lasted 2 hr. daily. On the first day of the fourth week the rats were placed on a straight alley runway in the vivarium and allowed to play freely on it. This procedure continued for three more days. On the next day, prior to their regular feeding, the animals were taken to the experimental room, where a simple elevated T maze (2) was located.

Starting on this fifth day after preliminary handling the animals were run for ten massed trials (correction procedure) per day. On the first trial each day food was found only at the right end of the maze, the left end being blocked. On the second trial food was to the left; on the third to the right; etc. Thus, the animals were forced to learn a simple alternation problem. The room had extensive extramaze environment (6).

The criterion for "learning" consisted of ten consecutive errorless trials on one day. On the day after reaching this criterion, the *S*s were given seven trials. If during these seven trials any of the animals had made a mistake, it would have been given three more trials and continued with ten trials daily until it again reached the criterion. No animal in the population made such an error.

This seventh trial was the crucial one. On this trial the animal turned right at the choice point. *After* the right turn but *before* the animal reached the curtain in front of the goal box, i.e., before it reached the *place* of the food, it was picked up and returned to the starting position. Note that the turning response for the trial had been completed. The direction in which the animal turned at the choice point on the eighth trial was recorded for each rat.

RESULTS

Twelve of the 15 rats responded on the test trial by turning to the right, i.e., in the same direction in which they had turned on the previous trial. Five animals, including the 3 which had turned left, exhibited extensive VTE behavior at the choice point. The other 10 animals appeared to run unhesitatingly to the right. The median number of trials taken to reach the criterion for all animals was 90, with a range of from 60 to 140 trials.

Assuming the null hypothesis to be a probability of .5 of returning to the same alley, we would expect a value as large as 12 out of 15 by chance only once in more than fifty experiments. On the basis of other research, especially that dealing with reactive inhibition (4) and spontaneous alternation (3), this null hypothesis is probably an overly stringent test for the experimental data.

DISCUSSION

Since the animals were removed from the maze and restarted *after* having made a turning response but *before* having reached the food place, we would expect, if they were alternating turning responses, that they would, on the next trial, turn to the left. However, if the rats were learning to alternate the *place* to which they went to find food, we would expect that having been interrupted before completing this "response" on the next trial they would turn right, which is what they did.

The experiment strongly suggests that the response which was being learned was the act involving the reaching of the food place. This result is supported by the work of Glanzer (3) in his studies of spontaneous alternation, and suggests that the definition of a response as a *pure* motor phenomenon is too restrictive.

The results can best be interpreted by saying that 10 of the 15 *S*s were learning to alternate the food place on each trial. The other 5 were probably traumatized by the interruption, as evidenced by the increased VTE's, and were probably displaying random behavior at the choice point.

There is one possible control which can justifiably be considered in the present research. It has been suggested that perhaps the right-turning tendency of the rat was stronger than the left-turning tendency, even though strict alternation was employed, because the *first* trial for each block of ten trials was a right turn. Therefore, if interruption occurred following the "stronger" right-turning trial, we might expect that any "disruption" which ensued would act to make the rat revert to the stronger of the two responses on the next trial, i.e., also a right turn.

There certainly appear to be counterarguments to this proposal. For example, why should not the *last* trial of each block of ten, which is a left-turning trial, receive additional increments of strength? However, an empirical answer is to be preferred for questions of this kind.

To this end, 15 additional rats of the same strain as those reported in the previous experiment were given training identical to that of the first group. The crucial trial, however, for 5 rats was the sixth trial, for another 5 it was the seventh trial (i.e., the same as the previous group), and for the remaining 5 animals it was the eighth trial. This meant that 10 *S*s were interrupted following a left-turning trial, while 5 were interrupted following a right-turning trial. Those interrupted on the seventh or right-turning trial were incorporated to provide a control over differences which might accrue to this new group by virtue of increased skill on the part of *E*, or their birthdates.

The median trials required to reach the criterion for all *S*s was 90 with a range from 60 to 160. Eleven of the 15 rats in this group turned in the same direction as they had on their previous trial. For the 5 rats interrupted on the seventh (right-turning) trial, 3 turned right. Eight of the other 10 rats turned left after being interrupted following a left turn (5 from the group of 5 interrupted on the sixth trial and 3 from the eighth-trial group). The probability of 11 out of 15 turning in the hypothesized direction by chance alone is less than .05.

The only other explanation which would appear to vitiate the spatial hypothesis is suggested by the results of certain experiments on the resumption of interrupted tasks. The animals may have been responding to a newly instigated drive or "tension" to complete the unfinished task. An experiment to test this hypothesis is presently in progress in the animal laboratories of the University of Pennsylvania.

SUMMARY

1. An experiment was conducted to test whether animals learn to alternate places or responses.

2. Thirty rats were trained on a simple T maze in a rich extramaze environment to learn a simple alternation problem to a criterion of ten perfect trials.

3. After they had reached the criterion, the animals were interrupted during one of their trials and restarted.

4. Twenty-three of the 30 animals responded by turning in the same direction as that on the interrupted trial.

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CHOICE ALTERNATION: I. STIMULUS VS. PLACE VS. RESPONSE

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"Spontaneous alternation" is a descriptive term which has been applied to the often observed tendency of rats to behave in an orderly rather than a random fashion when presented with a two-choice alternative more than once in close succession. Empirically, if an animal turns left in a T maze on its first trial, and if it is immediately returned to the starting point, the probability is quite high that it will turn right on the second trial.

This systematic tendency to alternate choices has assumed considerable theoretical importance. Solomon (7) related it to Hull's "reactive inhibition" (I_R). Montgomery (4, 5, 6) found the phenomenon related to the stimulus present and attempted to explain it as a manifestation of exploratory behavior. Glanzer (1, 2) independently verified Montgomery's findings and explained the behavior in terms of "stimulus satiation."

The present experiment stems from the logic and methods used by Montgomery and Glanzer. Both experimenters performed, among others, an experiment based on this kind of reasoning. Suppose we have a T maze with one arm painted white and one painted black. If an animal is placed in such a maze and turns left to the white stimulus, and on a second trial alternates and thus turns right to the black stimulus, it has alternated both the response (L, R) and the stimulus (w, b). It can be seen that the stimulus and the response in such a situation are confounded.

If one asks the question, "Is the animal alternating with respect to the stimulus or to the response?" it is necessary to arrange a situation in which the animal can do either one but not both.

Both Montgomery and Glanzer achieved this objective by using a +-shaped maze. This was accomplished by adding an additional starting stem apposed to the original one. Now if an animal turns left to the white (L, w) on the first trial, it can be placed at the other starting stem on the second. This time *S* may turn to the right and return to the white (R, w) or turn to the left and go to the black (L, b). In the first instance *S* would be alternating the response (L, R) but repeating the stimulus (w, w), and in the second instance *S* would be repeating the response (L, L) but alternating the stimulus (w, b). In both studies the tendency to alternate the stimulus was pronounced, and the response as a determiner of alternation seemed of little importance.

THE EXPERIMENTAL QUESTION

A further question could be asked of this situation: Is the observed alternation with respect to the black and white stimuli of the inside of the maze, or is the animal simply going to another place in the room?

This question can be answered in the following way. In the original experiments on spontaneous alternation as analyzed above, stimulus and response were unconfounded by Montgomery and Glanzer by presenting the animal with a situation in which it could alternate one but not both. In these designs, however, stimulus and place were still confounded. That is, the animal could alternate place plus the stimulus or the response:

$$PS \text{ or } R.$$

Stimulus and place can be separated by pitting either one against the other plus the response, thus:

$$RS - P$$

and

$$RP - S,$$

and with the Montgomery-Glanzer combination, the relative influence of the three possible determiners of alternation can be determined.

The animal can be offered these alternatives as shown in Figure 1. With the maze in the standard position the animal can be started

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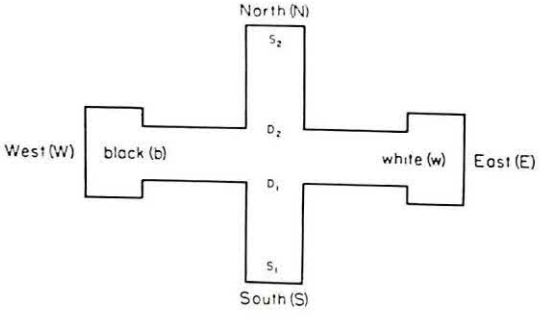
[1] This study was supported in part by a grant from the Horace Rackham School of Graduate Studies at the University of Michigan. The animals were run by A. J. Karoly.



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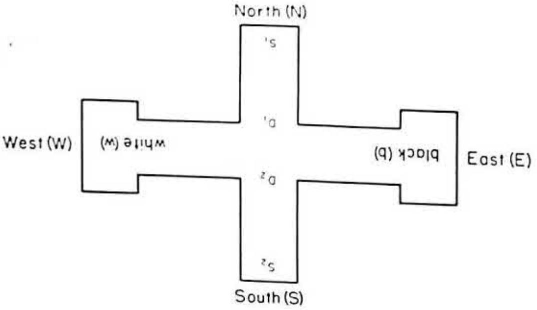

ROTATED

FIG. 1. Diagram of experimental maze showing relation between alternate starting positions (s_1 and s_2), one of which was closed off on each trial; color of alternatives; and spatial positions when in the standard and rotated positions. See text for explanation.

twice from the south (S) and at (s_1) both times. If *S* turns left to the black and thus goes to the west (L, b, W) on the first trial, when *S* is presented with its second trial, it must go either left, black, west (L, b, W), or it can go right, white, east (R, w, E). If *S* does the former, it repeats response-stimulus-place, and if *S* does the latter, it alternates all three:

RPS – O.

If *S* is placed at (s_1) on the south (S) on the first trial and at (s_2) at the north (N) on the second with the maze in the standard position, then response is pitted against stimulus and place as in the Montgomery and Glanzer situations. Thus:

PS – R.

If *S* is started at (s_1) at the south (S) on the first trial and before its second trial the maze is rotated 180°, and if *S* is started again at the south (S) but this time at (s_2), then *S* has this alternative. If *S* goes left to the black and to the west (L, b, W) on the first trial, it now may go left, white, and west, (L, w, W), or it may go right, black, and east (R, b, E). In the former, *S* will be alternating the stimulus but repeating the response and the place. In the latter it will be alternating the response and the place but repeating the stimulus. Thus:

RP – S.

Lastly, if *S* is started as before at (s_1) at the south (S) on the first trial and the maze is now rotated 180°, and on the second trial it is started from (s_1) again but this time from the north (N), the following can happen. If its first choice was left, black, west, (L, b, W), on its second trial *S* can turn right, white, west, (R, w, W), or it can turn left, black, east, (L, b, E). If it does the former, *S* would be alternating response and stimulus and repeating place, or if it does the latter, it can alternate place and repeat stimulus and response. Thus:

RS – P.

By using north (N) as a reference point, instead of south (S) as above, each of these four conditions can be repeated, making a total of eight conditions.

METHOD

Subjects

The *S*s for this experiment were 24 experimentally naive male albino rats. The *S*s all came from the same colony, were all born on the same day, and were approximately five months old at the time of the experiment.

Apparatus

The apparatus used in this experiment was a **+** maze as shown diagrammatically in Figure 1. The **+** maze, however, was always used as a **T** maze. This was accomplished by lowering either of the doors, D_1 or D_2, before the start of each *S*'s run. The entire maze in this experiment was placed on a large plywood board with wheels attached, so that the maze could be rotated on a track that was fastened to the table.

The maze had wooden walls 4 in. high by ½ in. thick and a mesh wire floor and roof. The mesh roof permitted the *S*s to see anything in the room above about the 6-ft. level. An 18-in.-square cheesecloth screen was fastened to the maze on the outside of each starting box so that *S*s could not see *E* but which allowed *E* to see where *S* was in the maze. The entire maze was set about 4 in. above the plywood board. The maze pathway was 4 in. wide throughout. The starting arms were 18 in. long from the choice point to the end of the starting box. The goal arms were 18 in. long from the choice point up to the door at the entrance to the goal box. The starting boxes were 6 in. by 4 in., and the goal boxes were 9 in. by 6 in.

In order to prevent retracing and to block off the entrance to the starting arm not in use, guillotine-type doors made of Masonite were used. These doors were situated at the entrances to each goal box and each starting box as well as on all four sides of the choice point.

Both the wood and wire mesh of the entire outside of the maze, as well as the inside of the starting arms and starting boxes, were painted a flat gray. The goal arms and goal boxes were made clearly distinct by painting the entire inside of one flat black and the other flat white. Furthermore, the coarseness of the wire mesh was different in each goal arm for a distance of 12 in. on either side of the choice point. That is, the black arm had mesh of four wires to the inch for both roof and floor, whereas the white arm had mesh of two wires to the inch. The gray portion of the maze, along with the remainder of the exit arms, had mesh of three wires to the inch.

The experimental room was a small room approximately 8 ft. by 8 ft. with a ceiling 9 ft. high. The north and east walls were of cement block painted a cream color. The west and south walls were of a metal panel material painted a flat gray. The door was situated at the center of the south wall, and was painted a rusty red color. There was a small ventilation register, painted to match the gray wall, just above and west of the door. There were no windows in the room. The table on which the maze rested was situated just northwest of the exact center of the room; and, therefore, the "white" fluorescent ceiling light was not directly over the maze.

Procedure

The experimental procedure consisted of an operationalization of the logical procedure described earlier in reference to the experimental question. With two starting places (S and N), two starting alleys (s_1 and s_2), and the possibility of rotation or nonrotation between the first and second members of a pair of trials, eight conditions are permitted. These eight conditions are specified in Table 1. As can be seen in the last column of this table, these eight conditions permit two tests each of four different combinations of these three sources of alternation determination.

For example, in Condition A, the animal has a choice of alternating all three at once (response, stimulus, and place) or nothing, that is repeating all three. This is tested twice, once starting from the north starting alley (N) and once starting from the south starting alley (S).

The animals were given four days of handling prior to the experiment in order to tame them. The prehandling consisted of 22 hr. of food deprivation and running the rats to food on either end of a board stretched between chairs in the cage room. The rats had no experience in the maze. They were then divided, by selecting every eighth rat, into eight groups of three rats each so that each group could be run under a single different condition each day.

TABLE 1

Design of Experimental Conditions

Condition	1st Trial Starting Place Stem	2nd Trial Starting Place Stem	Alternation Choice
A	S s_1	S s_1	RPS or O
B	N s_2	N s_2	RPS or O
C	S s_1	N s_2	PS or R
D	N s_2	S s_1	PS or R
E	S s_1	S s_2	RP or S
F	N s_2	N s_1	RP or S
G	S s_1	N s_1	RS or P
H	N s_2	S s_2	RS or P

Each animal in each group was given two trials, one immediately after the other on each of 16 days. There was never any food in the experimental maze. On any given day each of the eight groups was run under a different one of the eight conditions. After 8 days, each rat had run under each of the eight conditions. After the first 8 days, the same procedure was repeated so that after 16 days of test trials, each rat had experienced each condition twice.

The animals were run daily between 4 P.M. and 6 P.M. and were fed daily rations of three Purina Chow pellets about an hour after running. The home cages for the rats were just outside the experimental room in which the rats were being run. Each rat was taken individually into the experimental room (the order of running was the same every day), given the two successive trials required by the single test condition, and returned to the home cage. Between these two daily trials, the rat was placed in a small individual cage (in the experimental room) for about 30 sec. while *E* adjusted the maze for the second trial.

RESULTS AND DISCUSSION

The results may be seen in Table 2. When the animals are permitted to alternate with respect to all three manipulable aspects of this situation simultaneously—response, stimulus, and place—77.1 per cent of the choice pairs are alternations and 22.9 per cent are repetitions. When place and stimulus together are pitted against the response, the tendency to alternate is essentially no different. This result confirms those of Montgomery (4, 5, 6) and Glanzer (1, 2) precisely. They found that the response seemed to be almost without influence as a determiner of alternation.

When the stimulus is separated out of the

11.8.90
990

TABLE 2

Comparisons of the Tendency to Alternate under Each of the Four Basic Conditions of the Study

Alternation Choice	Average Number of Alternations Per Animal	Total Number of Alternations in Group	Percentage of Alternations	Comparison*	t**	p
RPS	3.08 (a)	74	77.1	a-b	.16	n.s.
O	.92	22	22.9	a-c	4.31	.001
PS	3.04 (b)	73	76.0	a-d	3.12	.01
R	.96	23	24.0	b-c	4.17	.001
RP	1.83 (c)	44	45.8	b-d	2.74	.02
S	2.17	52	54.2	c-d	2.31	.05
RS	2.33 (d)	56	58.3			
P	1.67	40	41.7			

* See text for explanation.

** These t values are calculated from the formula for t for correlated means given by McNemar (3, p. 226). They represent a slight underestimate of p, since the four opportunities each animal was given to respond to each of the basic conditions involved a repetition of a pair of trials where one of the pair was started from one starting alley and the other member of the pair was started from the other. This amounts to an experimental control not statistically controlled, and enters the error term with a consequent spurious reduction in the obtained t value. With an N of 24, the df is 23.

complex, however, and is pitted against the response and place together, a statistically significant difference is found (a-c comparison in Table 2). Likewise, when place is independently separated from the complex (a-d comparison), the difference is statistically significant. The comparisons between the response and stimulus as determiners of alternation (b-c comparison), response and place (b-d comparison), and stimulus and place (c-d comparison) indicate that of the three the stimulus is most important, place is second, and response last. Furthermore, all these comparisons are statistically significant.

While the data reported here do not directly support it, comparisons of these data with others suggest that the effectiveness of any one class of determiners of alternation could be manipulated almost at will.

The stimulus, which as used here means the intramaze stimuli, could be made maximally important by increasing the distinctiveness of the two sets of stimuli. The place cues could be maximized by arrangements of extramaze stimuli designed to make place distinctive. The general principle would be that choice alternation will be at a minimum when the stimuli relevant to the two alternatives are the same and will increase as the two sets of stimuli are made increasingly distinctive. Furthermore, alternation with respect to different aspects of the stimuli relevant to the two alternatives can be differentially manipulated to the extent to which the stimuli can be differentially manipulated with respect to distinctiveness. Increasing the effectiveness of the response as a determiner of alternation could be accomplished by analogy with the principle stated above by making the physical responses to the two sides as qualitatively different as possible in terms of their proprioceptive returns. This possibility is the subject of a further experimental paper in this series.

Hull's "reactive inhibition" concept (I_R) has been applied to data of this kind. As an empirical description of a class of behavioral change which occurs as a function of time, Hull's notion is not contradicted. As a theoretical construct relating that change to the response, to the exclusion of the stimulus, its applicability to choice alternation seems clearly brought into question by these findings as it has already by Glanzer and Montgomery.

Glanzer's "stimulus satiation" concept is applicable to these data if one treats stimulus and place as intramaze and extramaze stimuli. The possibility that the response has some influence on alternation would not be handled by Glanzer's theoretical formulation. Montgomery's "exploratory drive" seems indistinguishable in its predictions from Glanzer's "stimulus satiation."

SUMMARY

Twenty-four naive albino rats at five months of age were tested in a + maze with a design which permitted the animal to alternate with respect to the response (left-right), the intramaze stimuli (white-black), or place (east-west) in combinations which yielded an assessment of the relative importance of each of these possible determiners of choice alternation. The response was found to have little, if any, importance; place had a considerable importance; and the stimulus had more importance than place. The conclusion was reached, partly on the basis of these data, that the relative importance of

each of these variables could be manipulated almost at will. Hull's "reactive inhibition" concept fits these data as an empirical description, but not as a theoretical construct. Glanzer's "stimulus satiation" concept and Montgomery's "exploratory drive" both fit as long as the response plays little role, as it does in these data.

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CHOICE ALTERNATION: II. EXPOSURE TO STIMULUS OR STIMULUS AND PLACE WITHOUT CHOICE

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When rats are placed at a choice point more than once in quick succession, the probability is quite high that they will alternate, or choose on the second trial the opposite of their choices on the first trial. When Montgomery (3, 4, 5) and Glanzer (1, 2) gave animals the opportunity to alternate the stimulus and repeat the response or to alternate the response and repeat the stimulus, the stimulus proved to be the important determiner of behavior. When Walker, Earl, Dember, and Karoly (6) made a further separation of the determiners of alternation into stimulus, place, and response, they found that of the three, stimulus was most important, place, moderately important, and response, least important.

Glanzer (1) treats his data in terms of "stimulus satiation" as if alternation behavior was a function of a decrement in the tendency to respond positively to the black or white stimuli of the inside of the maze. Place can be treated as extramaze stimuli and the results obtained by Walker, Dember, Earl, and Karoly handled within the framework of Glanzer's theory. This treatment would reason that intramaze stimuli and extramaze stimuli are simply two different sources, each of which contributes a share in the determination of alternation. It is an easy implication that exposure to the two sources of stimuli could be independent of each other or of the maze itself without altering their effect on the tendency of the animal to approach or to avoid them.

It seems to follow, for example, that if an animal is exposed to a white stimulus for a period of time and then introduced to a T maze with one white and one black alternative, it should choose the black alternative, since the previous exposure should have led to "stimulus satiation" for white.

This paper is concerned with two experiments designed to test this proposition. In Experiment I,[2] the animals were exposed to white, gray, and black boxes outside the maze for varying periods of time, and they were then introduced to a T maze with black and white alternatives. In Experiment II,[3] the animals were placed in the black and white goal boxes of the maze itself for a period of time and then introduced at the starting point. By rotating the maze between the exposure and the test, the animal could be presented with a chance to alternate stimuli and thus repeat place, or to alternate place and thus repeat stimuli. The two experiments together permit a contrast of "the stimulus not in this place" with exposure to "the stimulus in this place."

METHOD

Subjects

Experiment I. The *S*s were 6 experimentally naive, male rats. They were albino rats from the colony of the University of Michigan, were all born on the same day, and were approximately 5 months old at the beginning of the experiment. In the subsequent partial replication of this experiment, 40 naive white rats approximately 4 months old were used.

Experiment II. The *S*s were 24 experimentally naive, male albino rats which were approximately 9 months old at the beginning of the experiment. In the first partial replication, 12 more rats approximately 6 months old were used, and in the second partial replication, 20 more naive albino rats were used.

Apparatus

The apparatus for both these experiments was the same as that used by Walker, Dember, Earl, and Karoly (6).

In Experiment I the apparatus was used as a simple T maze, with one white and one black alternative. In addition, a "stimulus exposure" box was used. Originally this box had been a compartmentalized carrying cage with sections which measured 4 in. by

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[1] This study was supported in part by a grant from the Horace Rackham School of Graduate Studies at the University of Michigan.

[2] This experiment was run by Andrew J. Karoly. A partial replication was run by William N. Dember.

[3] This experiment was run by Stewart E. Fliege. Two partial replications were run by William N. Dember.

5 in. by 5 in. Two were painted black, two were white, and two were gray. After Condition 1 was completed, partitions were removed making three large compartments measuring 8 in. by 5 in. by 5 in. one of each color.

In Experiment II the maze was used as a + maze. This maze could be rotated. If an animal is placed in the black goal box on the west side, and if after *S* is removed the maze is rotated 180° before the animal is placed at the starting point, *S* can either go to the white arm now at the west, avoiding the original stimulus and approaching the original place, or *S* can go to the black arm now on the east side and thus avoid the original place and approach the original stimulus.

Procedure

The animals in both experiments were given the same pre-experimental experience. This consisted of four days of handling in order to tame them. During these four days the animals were food deprived for a period of 22 hr. and then permitted to run back and forth on a board suspended from two chairs to get food. This experience took place in the cage room and the animals had no prior experience in the experimental maze.

Experiment I. The animals were run under four different conditions in which the size of the exposure box or the time of the exposure was varied. The conditions were as follows:

Condition 1. Thirty-minute exposure in small boxes. Four days.

Condition 2. Thirty-minute exposure in large boxes. Four days.

Condition 3. Fifteen-minute exposure in large boxes. Two days.

Condition 4. Thirty-second exposure in large boxes. Two days.

Two of the six animals were exposed to each color on each of the experimental days, and each pair was shifted to a different color each day.

The animals were run daily between 3 and 4 P.M. and were fed their daily ration of three Purina Chow pellets about an hour after running. They received no food in the maze. Each animal was taken from its home cage and placed in one compartment of the stimulus exposure box which was left in the cage room. After the predetermined period of exposure, the box was carried into the experimental room, and each animal was given one trial in the T maze. In the 30-sec. exposure condition, the animals were placed in the exposure box singly and tested before the next animal was removed from the home cage.

Because of the obvious lack of any tendency to choose the opposite of the exposure color during the first eight days, on days 9, 10, and 11 the animals were given a second choice immediately after the test trial. This made it possible to test whether these animals under these conditions would alternate on successive "choices" as had been previously ascertained. In the partial replication, the conditions were the same as in the original experiment. Half the animals were exposed to black, half to white, and the exposure time was 45 sec.

Experiment II. The animals were placed in one of the two goal boxes of the experimental maze for 45 sec. They were then removed to a small holding cage for 30 sec. while the maze was being adjusted, and then introduced at the starting point. With two colors (black and white), and two places (east and west) where the exposure could occur, there were four exposure conditions. For each exposure condition, the test trial could be started at the north or at the south, and the maze could remain stationary or could be rotated between exposure and test. This made four test conditions. Thus there was a total of 16 conditions. In half these conditions, when the maze is stationary between exposure and test, the animal may approach both the stimulus and place of the exposure period or avoid both. In the other eight conditions, *S* may choose to approach the same place and avoid the exposure color, or it may choose to avoid the same place and approach the exposure color.

The animals were divided into eight groups of three animals each. Each group of animals was run through all 16 conditions, and on any given day, each of the eight groups was experiencing a different condition.

The animals were run daily from 10:00 A.M. to noon. They were run under approximately 22 hr. of food deprivation. Each day their home cages were transported on a cart from the living area to a place just outside the experimental room. After all animals had been run, the cages were taken back to the living area. They were fed their daily ration of three Purina Chow pellets approximately 1 hr. after running. They received no food in the experimental maze. In the first partial replication, each animal was exposed for 45 sec. to one goal box and then placed in the starting box. Each was exposed to a different stimulus-place combination on each of four days. In the second partial replication half the animals (10) were exposed to one goal box, half to the other. They were tested once.

RESULTS AND DISCUSSION

Experiment I was designed to ascertain whether exposure to a white stimulus disassociated from the T maze would influence the choice of a white or a black alternative in the maze. The results may be seen in Table 1. It is quite clear in both the original results and in the replication that exposure to one of the alternative stimuli outside the maze creates no predisposition for the animal to choose the alternate stimulus in the maze. A test of the significance of the difference between the original experiment and the replication yields a *t* of .39. One additional result should be mentioned. When it became clear in the original experiment that pre-exposure was not influencing the behavior as might have been expected from a "stimulus satiation" theory, each of the animals was given a second trial after the test trial for three days. This per-

TABLE 1

Experiment I—Stimulus Exposure, Showing Turns Toward or Away from Exposure Color*

Experiment	Number of Turns	Percentage of Turns
Original experiment		
Condition 1		
To exposure color	9	56.3
Away from exposure color	7	43.7
Condition 2		
To exposure color	7	45.7
Away from exposure color	9	56.3
Condition 3		
To exposure color	5	62.5
Away from exposure color	3	37.5
Condition 4		
To exposure color	5	62.5
Away from exposure color	3	37.5
All conditions		
To exposure color	26	54.2
Away from exposure color	22	45.8
Partial replication		
To exposure color	20	50.0
Away from exposure color	20	50.0

* The results obtained when exposure was to gray are not reported here. They show a slight tendency for the animals to prefer the black alternative, a tendency controlled out of the results reported.

mitted us to "sample," so to speak, the alternation tendency of these animals under these conditions in the traditional way. Of 18 opportunities to alternate choices, 16 or 89 per cent were alternations and only 2 or 11 per cent were repetitions.

The second experiment was designed to ascertain whether exposure to the "stimulus in this place" could lead to a tendency to avoid the exposure stimulus even though there was no apparent tendency to avoid the exposure stimulus in Experiment I. It also permitted an assessment of the relative influence of stimulus and place should there be any.

These results may be seen in Table 2. Placing the animal in one of the goal boxes had little effect on a subsequent choice. A test of the significance of the difference between the results in Experiment I, with exposure to the stimulus alone, and the results in Experiment II, with exposure to both stimulus and place, is not significant despite an exceptionally large N (see Table 3). The findings in Experiment II do not differ significantly from random choices. Thus one cannot safely assume even a slight tendency to avoid the box (stimulus and place) to which the animal was exposed. If one should reason that a more extensive test would have revealed a small reliable difference, the most striking characteristic of the results would still be the smallness of this difference in comparison with that found in the Walker, Dember, Earl, and Karoly study (6). A comparison of the three experiments may be seen in Table 3. There is a significant difference between the results when the animal is allowed to choose one alternative and then given another choice as compared with the results when the animal is placed in the goal box for a comparable period and then given one choice.

The separation of stimulus and place would have had significance in Experiment II, had there been a marked and significant tendency to avoid the exposure condition. As it is, very little can be said. If there is a tendency to avoid the exposure condition, it is the stimulus and not the place which is being avoided. Since one cannot safely say that there is any

TABLE 2

Experiment II—Choices to and Away from the Goal Box to Which the Animal Had Been Exposed (Stimulus and Place), and the Choice Between Stimulus and Place when the Animal May Approach Either but not Both

Experiment	Number of Choices	Percentage of Choices
Original experiment		
Choices toward exposure		
Stimulus and place	83	43.23
Choices opposite exposure		
Stimulus and place	109	56.77
Choices opposite exposure		
Place	82	42.71
Choices opposite exposure		
Stimulus	110	57.29
First partial replication		
Choices opposite exposure		
Stimulus and place	24	50.0
Choices toward exposure		
Stimulus and place	24	50.0
Second partial replication		
Choices opposite exposure		
Stimulus and place	9	45.0
Choices toward exposure		
Stimulus and place	11	55.0

TABLE 3

Comparative Tendencies to Choose the Opposite of the Exposure Condition

(Original experiments and replications are combined.)

Exposure Condition	Number of Animals*	Number of Choices	Percentage of Choices
1. Exposure to stimulus outside of maze			
Opposite exposure condition	22.5	42	47.7
Toward exposure condition	23.5	46	52.3
2. Exposure to stimulus and place in maze			
Opposite exposure condition	31	142	54.6
Toward exposure condition	25	118	45.4
3. Self-exposure to stimulus, place, and response in maze			
Opposite exposure condition	22	74	77.1
Toward exposure condition	2	22	22.9

Comparison	x^2	p
1 and 2	.20	.65 (approximate)
1 and 3	10.67	.001
2 and 3	8.35	.01

* After it was established that there was no difference between the original experiments and their replications, all animals were classified as an "Opposite" or a "Toward" animal. Ties were divided equally. There were three ties in Condition 1, ten in Condition 2, and two in Condition 3.

tendency to avoid the exposure condition, one cannot safely attempt to apportion the determination of this tendency.

These results taken together seem to permit several conclusions. When given two choices in close succession in a T maze, animals tend on the second trial to avoid the situation to which they were exposed by their own choice on the first. The determiners of this tendency (stimulus, place, and response) can be assessed with respect to their relative roles. However, when the active choice of the animal is omitted and *S* is exposed either to the color of one of the alternatives alone but disassociated from the maze, or when *S* is exposed to the color and place together by being placed in the goal box of the maze itself, little or no tendency to avoid the exposure condition is demonstrated.

Thus, while attempts to assess the relative degrees to which stimulus, place, and response determine alternation behavior show that the stimulus is by far the most important, exposure to the stimulus alone has no influence. While stimulus and place account for virtually all the variance here as opposed to response in the Walker, Dember, Earl, and Karoly (6) experiment, exposure to stimulus and place disassociated from the actual choice of the organism has little if any effect. Choice cannot be identified with response in the sense of left and right turns, for response in the latter sense was shown in the Walker, Dember, Earl, and Karoly experiment to play a relatively unimportant role.

What then is the meaning of choice? These experiments were designed, in a sense, to show what it could not be and not what it is. Our preference at the moment and on the basis of these experiments alone is to say that if an animal is given what anthropomorphically seems to it to be the same decision twice, *S* is likely to choose two alternatives rather than one. In the Walker, Dember, Earl, and Karoly experiment, we are assessing the way in which the animal "saw" its first decision. Most saw it as a choice of colors, some saw it as a choice of places, virtually none saw it as a choice of response.

In the two experiments reported in this paper, the animal was given only one choice, and its prior experience, which did not involve a choice, did not, therefore, show much influence.

Thus we can tentatively conclude on the basis of these experiments, that it is a choice that is being alternated in "spontaneous alternation" studies, and that the various factors that have been studied must be relevant to the choice in order to influence the tendency to alternate. While this conclusion seems satisfactory for these data, the requirement of choice limits the generality of the principles involved. Further studies will undoubtedly yield a more precise description of the necessary conditions for influencing a subsequent choice.

SUMMARY

Two experiments were performed to ascertain whether exposure to either the black or white stimuli of the maze, but outside the maze, or exposure to the black or white goal boxes of the maze itself would influence a subsequent free choice of the animal when introduced into a T maze with black and white alternatives.

In Experiment I, six animals were detained

in exposure boxes under four different conditions. The conditions were: (*a*) 30-min. exposure in small boxes, (*b*) 30-min. exposure in large boxes, (*c*) 15-min. exposure in large boxes, and (*d*) 30-sec. exposure in large boxes. In 54.2 per cent of the subsequent choices, the animals approached the exposure color. A replication involving 40 animals with 45-sec. exposure produced a 50 per cent choice of the exposure color. The conclusion is drawn that such pre-exposure to the stimulus color had no effect on the subsequent choice.

In Experiment II, 24 animals were placed for 45 sec. each in one of the goal boxes, and after a 30-sec. pause placed at the starting point. There is no demonstrable tendency for these animals to choose the opposite of the exposure condition. A partial replication involving four tests each for 12 animals and another involving one test each for 20 animals confirmed the finding of no effect of such exposure.

There is a significant difference between each of these results and the large tendency to alternate obtained by Walker, Dember, Earl, and Karoly (6) when the animal first "chooses" and is thus exposed to one of the alternatives and is then given a second opportunity to choose.

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A CONSIDERATION OF THE OBJECT-QUALITY DISCRIMINATION TASK AS A DEPENDENT VARIABLE[1]

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Consistency of individual performances is an important requirement for most dependent variables. If one measures performance on a relatively unreliable test, the probability of obtaining significant results attributable to the effects of an independent variable is poor. Lack of internal consistency in the dependent variable leads, in general, to an underestimate of the action of an independent variable. In the investigation of learning, however, a constant level of performance scores is neither expected nor desired. By definition, changes in performance are expected between repeated tests or trials. When a learning task is employed as a measure, the more sensitive task is the one on which *S*s' ranks remain relatively constant from trial to trial or from one stage of learning to another. A task on which *S*s vary widely in rank position from one stage of learning to another will be an insensitive indicator of the action of an independent variable.

Carr (2, 3) has emphasized some of the practical and theoretical hazards that often occur in interpreting learning task reliabilities; however, if precautions are taken, the reliability figures undoubtedly contribute materially to the use of the task in question. In addition, the availability of reliability coefficients makes it possible to assess the effects of minor changes in the apparatus. For example, both Leeper (8) and Ruch (10) have demonstrated the increased reliability of animal mazes when retrace doors are added. McNemar (9, p. 122) has discussed the problem of the meaningfulness of reliability determination for learning tasks.

The aim of the present investigation was to determine the reliability characteristics of the object-quality discrimination task in order to improve the usefulness of the test as a dependent variable.

METHOD

Subjects

The data used in this study were collected from 23 young rhesus monkeys weighing 5 to 9 lb. and having comparable experience and training in the laboratory. These animals were trained in groups of 6, 8, and 9. Each group was trained as a unit on the object-quality discrimination task. Although all the groups were not trained during the same calendar months, they were tested during the period from November, 1950 to October, 1951.[2]

Apparatus

Discrimination learning was conducted in the Wisconsin General Test Apparatus (WGTA) described by Harlow and Bromer (7). The essential elements of the WGTA are a restraining cage for the monkey; a stimulus tray which can be pushed forward within the animal's grasp; an opaque screen which, when lowered, prevents *S* from observing the baiting of the objects; and a one-way-vision screen through which *E* can observe *S*.

The stimuli to be discriminated were 320 pairs of stereometric objects similar to those used by Harlow (5). When more than 320 problems were presented, the series was repeated starting with the first objects.

Procedure

Preliminary training. Each group of monkeys was given a laboratory adaptation period of approximately three weeks before the beginning of the training trials. During this period the monkeys were observed carefully for indications of illness or physical impairment. During the adaptation period they were partially trained by *E*, who fed each animal by hand several times daily.

After the animals had become adapted to living in the colony, preliminary training trials were conducted in the WGTA. During the course of a six-week period the monkeys were taught to displace stimulus objects on the movable tray in order to receive food rewards. The initial hesitation and withdrawal responses to the various movements and noises of the apparatus were overcome during preliminary training.

Object-quality discrimination learning. The only pertinent change in general test procedure from that described by Harlow (6) was that each object-quality problem was presented for only three rather than six trials (1).

All groups were given 576 object-quality problems.

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[1] This investigation was supported in part by research grant No. M-487 (C) from the National Institute of Mental Health, Public Health Service.

[2] Some of the data herein reported were collected by H. W. Braun and H. W. Barnes.

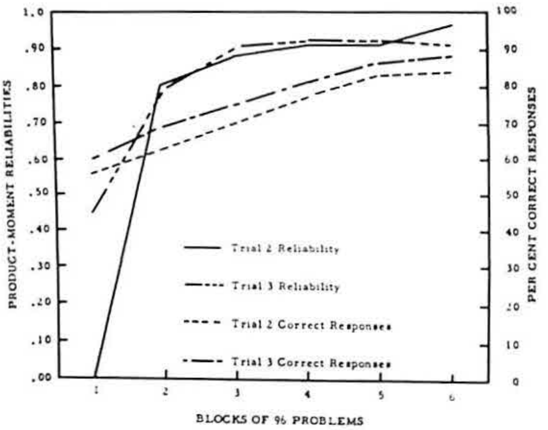

FIG. 1. The intrablock reliabilities and percentage of correct responses for trial 2 and trial 3 of object-quality discrimination learning.

The stimulus objects and positional sequences used were identical for all animals. Eight three-trial problems were presented each day.

RESULTS

The reliability of performance on the discrimination task was calculated within each block of 96 problems for trial 2 and for trial 3. Since eight problems were given per day, 12 testing days were necessary to complete a block of 96 problems. The split-half reliabilities were determined by correlating the errors of odd and even days. The resulting reliability coefficients were corrected with the Spearman-Brown formula (9).

The corrected coefficients for the split-half reliability within each block of 96 problems are illustrated in Figure 1. The percentages of correct responses on the object-quality problems for trials 2 and 3 are also shown in Figure 1.

TABLE 1

Intercorrelations (Product-Moment) Between Trial 2 Performances on Successive Blocks of 96 Problems

Blocks of Problems	Blocks of Problems				
	2	3	4	5	6
1	.16	.13	.17	.10	.15
2		.82**	.58**	.52*	.41*
3			.79**	.56**	.48*
4				.83**	.73**
5					.95**

* Significant at the .05 level.
** Significant at the .01 level.

TABLE 2

Intercorrelations (Product-Moment) Between Trial 3 Performances on Successive Blocks of 96 Problems

Blocks of Problems	Blocks of Problems				
	2	3	4	5	6
1	.56**	.32	.16	.16	.01
2		.66**	.56**	.52*	.43*
3			.91**	.87**	.76**
4				.93**	.90**
5					.93**

* Significant at the .05 level.
** Significant at the .01 level.

Correlations were also computed for errors between the blocks of problems, i.e., each block was correlated with every other block of problems. Since these product-moment coefficients were calculated between blocks of problems, no correction factor was employed. These intercorrelations are presented in Tables 1 and 2 for trial 2 and trial 3 performances respectively.

DISCUSSION

As training progressed, the reliability within a block of 96 problems was found to increase rapidly in the case of both trial 2 and trial 3 performance (Fig. 1). Whereas the trial 2 coefficient for the initial block of 96 problems was .01, the reliability of performance on the final block of problems was 0.96. As could be anticipated, the reliability within the initial set of 96 problems was slightly higher for trial 3 performance than the corresponding value for trial 2.

If one is attempting to investigate the influence of an independent variable (e.g., a pharmacological agent) on the learning or retention of a discrimination task, it is desirable in many instances to introduce the independent variable before the asymptote of performance is reached or before overlearning has a chance to occur. One means of achieving this is to select a criterion of performance which the individual *S* must meet before it is placed in an experimental or control group. The criterion may be adjusted so that the sensitivity of the task as a measure of the effect of the independent variable is optimal. It is frequently desirable for theoretical or practical purposes to insure that all *S*s have received the same amount of practice or number of trials on the task in question. In this case, either a constant number of trials may be given or a group criterion utilized. Another technique that permits the introduction of the independent variable at any stage of the learning process is randomization. In order to utilize the randomization technique most efficiently, however, reasonably large groups of *S*s must be available for testing.

In the usual infrahuman primate experiment the number of available *S*s is limited. For this reason it seems desirable to utilize information regarding the tasks involved to assign *S*s into groups. Often, of course, the necessary information is lacking, and one must assign animals to groups randomly. In the case of object-quality discrimination behavior, however, a large number of *S*s has been tested in this and other laboratories. Data are available from which refined criteria for matching groups may be derived. The intercorrelations between blocks of successive problems provide an estimate of the size of the correlation figure which will be inserted into the standard error of difference formula for groups with similar distributions on a matching variable (9, pp. 339–340). Since use of this technique involves the loss of one degree of freedom, the intercorrelation between blocks must be judged high enough to produce a sufficient savings in the size of the standard error so that the loss of a degree of freedom is overcome. An idea of the relative advantage to be gained from matching groups over randomization is indicated by noting that a correlation of .71 leads to a reduction in error equivalent to that obtained by doubling the size of the samples. An intercorrelation of .87 diminishes the sampling error by one-half (9, pp. 340).

Both Edwards (4, pp. 288–295) and McNemar (9, pp. 336–341) have discussed the statistical and experimental considerations involved in the matching of groups. It would appear that appropriate use of the information concerning intercorrelations between successive blocks of problems on the object-quality discrimination task may increase its sensitivity as a dependent variable.

It should be pointed out that differences in the number of trials given per problem or in training technique would undoubtedly alter the intercorrelations between blocks of problems markedly.

SUMMARY

Twenty-three young rhesus monkeys were trained on three-trial object-quality discrimination. All the animals experienced 576 discrimination problems. The intercorrelations between successive blocks of 96 training problems were determined. In addition, the split-half correlations within blocks of problems were computed.

This information concerning the reliability and intercorrelations between successive blocks of problems may be used to determine when a group of animals should be assigned to subgroups for the application of an independent variable. Appropriate application of these data will tend to increase the sensitivity of this discrimination task as a behavioral measure.

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THE EFFECTS OF FIXED-RATIO RANDOM REINFORCEMENT ON RESPONSE LATENCY OF MONKEYS[1]

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The experimental data concerning partial reinforcement have been divided, on occasion (8), into three basic categories: acquisition, retention, and extinction. Those studies dealing with the acquisition of responses generally agree that 100 per cent reinforcement is more efficacious than partial reinforcement since the final training level is not only higher but is also reached more rapidly than it is for less frequent reinforcement (3, 4, 7). There is a reversal of proficiency, however, during the extinction series following performance or training under a partial reinforcement regime. Under such conditions extinction occurs more rapidly following 100 per cent reinforcement than it does under partial reinforcement schedules (5, 8).

Fewer studies have been concerned with the effects of various ratios of reinforcement on already established conditioned responses. Among those most pertinent to the present investigation is a study by Brogden (1), who found that with reinforcement ratios ranging from 20 to 100 per cent in 20 per cent increments the frequency of the conditioned response for any ratio never dropped below 80 per cent for any of the three types of conditioning studied: conditioned flexion reinforced by shock, conditioned flexion reinforced by food, and conditioned salivation reinforced by food. For conditioned flexion reinforced by food and conditioned salivation the 20 per cent reinforcement condition was significantly less effective than the higher ratios of reinforcement.

These findings of Brogden are in contrast with those of Butler, Settlage, and Harlow,[3] who studied the effects of 12.5, 25, 50, and 100 per cent reinforcement on the latency of an object-displacing response by normal monkeys and monkeys with bilateral destruction of the prefrontal areas. No differences were found among any of the reinforcement conditions for the operate group. The 12.5 and 25 per cent reinforcement conditions were found to be significantly less effective for the normal group in maintaining performance than the 50 and 100 per cent conditions, but no differences were found within the two lower or within the two higher conditions.

The experiments to be reported herein are part of a series designed to augment these data of comparative psychology through a more complete dimensional analysis of the relationship between the retention, or maintenance, of responses and ratio of reinforcement.

EXPERIMENT I

Method

Subjects. Eight experimentally naive rhesus monkeys (no. 174, 178, 179, 181, 182, 184, 185, and 187) were selected as *S*s for this study. All animals had been previously tamed and adapted to the experimental situation.

Apparatus. The Wisconsin General Test Apparatus (5, Fig. 1) was used throughout the experiment. It consists of a table placed in front of a barred restraining cage. Mounted on the table is a superstructure holding two movable screens, an opaque screen located just in front of the cage, and a one-way-vision screen located in front of *E*. A movable tray rests on a track on the table and can be advanced toward and withdrawn from the restraining cage. The tray contains a single food well $1\frac{1}{4}$ in. in diameter, with its center midway between the sides of the tray and $2\frac{1}{2}$ in. from the forward edge. An electrical circuit is incorporated into the apparatus to make possible accurate measurement of response latency. A single stimulus object is used in this experiment and when it is placed over the food well, a small metal pin is depressed, activating a microswitch and completing part of the circuit. Advancing the tray forward closes a second microswitch located 7 in. from the opaque screen and starts a Standard Electric chronometer. Displacement of the object breaks the circuit and stops the chronometer. With this apparatus, response latency can be recorded to 0.01 sec.

Experimental design. There were 11 conditions of fixed-ratio random reinforcement ranging from 0 per

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[1] This experiment is part of a dissertation conducted under the direction of Professor Harry F. Harlow and submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Psychology at the University of Wisconsin in 1953.

[2] Now at Purdue University.

[3] BUTLER, R. A., SETTLAGE, P., & HARLOW, H. F. The effects of partial reinforcement on normal and brain-damaged monkeys. Unpublished manuscript.

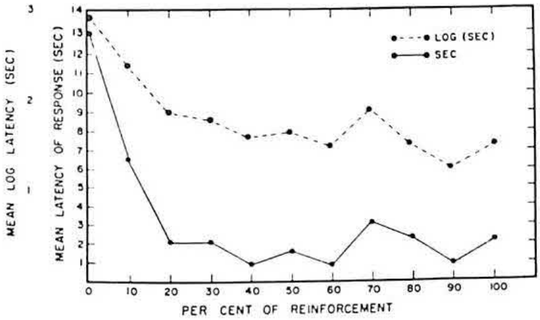

FIG. 1. Performance as a function of frequency of reinforcement.

cent to 100 per cent in 10 per cent increments. Each animal was tested on a given condition 50 trials a day for five consecutive days. The daily run of 50 trials was subdivided into five blocks of 10 trials each, and a predetermined frequency of reinforcement was assigned to each of these blocks. The sequence of presentation of the reinforcement conditions for each animal was randomly determined with the one restriction that the initial condition was never 0 per cent. Raisins were used as the food reward, and a trial was terminated if the animal failed to respond within 20 sec.

Preliminary training. The preliminary training regimen required that the animals displace a single object on a one-hole tray within a 10-sec. period for 95 of 100 trials on three of five successive test days.

Test procedure. Each monkey was brought into the apparatus room from the living quarters in a small transport cage. After being placed in the restraining cage, the animal was given four or five pieces of food, and testing began. The forward screen was lowered, and the block was placed over the empty or rewarded food well. The one-way-vision screen was lowered and the opaque screen raised, and the tray moved forward within the animal's reach. After the monkey displaced the block and took the food reward, if present, the tray was withdrawn, and the opaque screen was lowered. The *E* recorded the latency of the response and prepared the tray for the next trial.

Results

The mean latencies plotted as a function of the 11 conditions of reinforcement are presented in Figure 1. A log transformation was performed on the data to normalize the distribution, and a constant of 2.0 was added to eliminate negative log values.

The tests of significance by the analysis of variance technique are summarized in Table 1. The sources of Reinforcement Conditions, Animals, and Blocks within Days are significant at the .01 level of confidence. The means for the reinforcement conditions of 0, 10, and 90 per cent were found to differ significantly from the remaining means when the difference between means was analyzed by Tukey's (9) gap test. None of the means for the remaining percentages of reinforcement was significantly different from any other. The level of significance for the gap test was the *t* value for the .05 level of confidence.

In Figure 2 mean log latency is plotted as a function of blocks of trials. The mean log latency changes from 1.6715 for block 1 to 2.0278 for block 5. The test of significance of this variable presented in Table 1 shows that this over-all change in latency is significant at the .01 level when the Days × Blocks interaction is used as the error term.

EXPERIMENT II

Method

Subjects. Eleven experimentally naive rhesus monkeys (no. 211, 212, 213, 214, 215, 216, 217, 218, 219, 220, and 221) were used in this experiment. The adapta-

TABLE 1

Main Effects Tested over Appropriate Significant Interactions

Sources	*df*	Mean Square	*F*
Reinforcement Conditions	10	43.35	289.00*
Conditions × Days × Blocks	160	0.15	
Animals	7	11.04	138.00*
Animals × Conditions × Days × Blocks	1120	0.08	
Days within Conditions	4	0.70	6.36*
Days × Blocks	16	0.11	
Blocks within Days	4	9.11	82.8*
Days × Blocks	16	0.11	

* Significant at .01 confidence level.

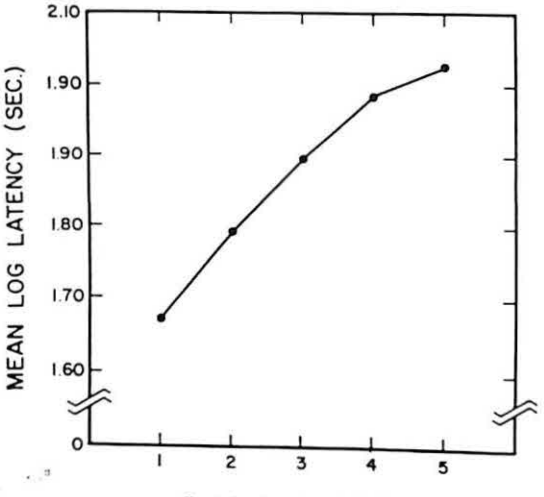

FIG. 2. Performance as a function of blocks of trials within days.

tion and taming experience of all animals was similar to that reported in the preceding experiment.

Apparatus and procedure. The apparatus and test trial procedures were identical with those described in the preceding experiment.

Experimental design. Six conditions of fixed-ratio random reinforcement were utilized, ranging from 5 to 30 per cent in 5 per cent increments. Each animal was tested on a given condition 60 trials a day for four consecutive days. The daily run of 60 trials was subdivided into three blocks of 20 trials each, and the predetermined frequency of reinforcement was assigned in each of these blocks in the same manner as described for Experiment I. All animals were tested under all conditions of reinforcement, and the sequence of conditions was randomly determined for each animal. Raisins were used as the food reward and a trial was terminated if the animal failed to respond within 20 sec.

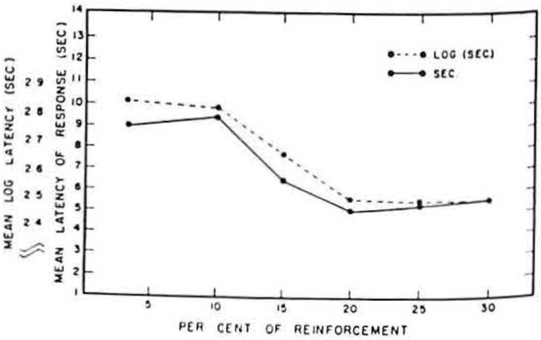

FIG. 3. Performance as a function of frequency of reinforcement.

Results

The mean latencies plotted as a function of the six conditions of reinforcement are presented in Figure 3. A log transformation was performed on the data to normalize the distribution, and a constant of 2.0 was added to eliminate negative log values. Examination of the figure reveals that the mean log latency ranges from 2.85 for the 5 per cent condition to 2.50 for the 20 per cent reinforcement ratio. From 20 per cent to 30 per cent little change in performance is apparent.

A summary of the analysis of variance is presented in Table 2. The main effects of Reinforcement Conditions, Animals, and Blocks within Days were found to be statistically significant at the .01 level of confidence.

The analysis of the difference between means by Tukey's gap test (9) revealed that the reinforcement conditions of 5 and 10 per cent could be separated off as a group. The mean

TABLE 2

Main Effects Tested over Appropriate Significant Interactions

Sources	df	Mean Square	F
Reinforcement Conditions	5	3.85	192.5*
Conditions × Days × Blocks	30	0.02	
Animals	10	7.05	3525.00*
Animals × Conditions × Days × Blocks	300	0.002	
Days within Conditions	3	0.04	1.00
Days × Blocks	6	0.04	
Blocks within Days	2	2.60	65.00*
Days × Blocks	6	0.04	

* Significant at .01 confidence level.

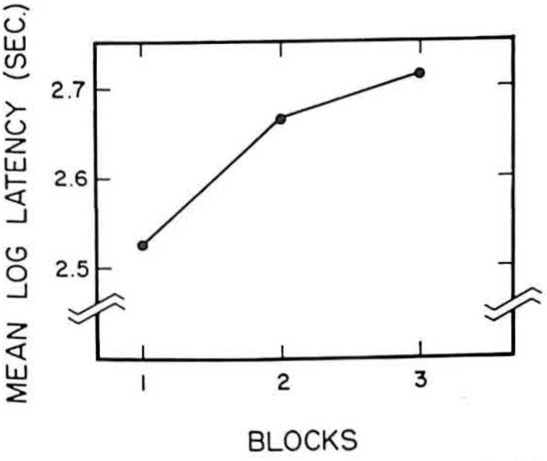

FIG. 4. Performance as a function of blocks of trials within days.

for 15 per cent was separated off from all other conditions and the means for the remaining conditions of 20, 25, and 30 per cent were separated off as a homogeneous group. The level of significance for the gap test was the *t* value for the .05 confidence level.

In Figure 4 mean log latency is plotted as a function of blocks of trials, and it may be noted that the latency changes from 2.52 for block 1 to 2.72 for block 3, a statistically significant change.

DISCUSSION

The data of the initial experiment indicate that a sharp transition in performance occurs at or around the 20 per cent frequency of reinforcement. These findings are corroborated by those of the second study, which was conducted to determine more precisely the portion of the function near the transition point. These results are in essential agreement with those of Brogden (1), and differ markedly from those obtained for acquisition and extinction as a function of various ratios of reinforcement.

Meyer[4] has found that monkeys can discriminate between a proportional reinforcement schedule of 60:40 per cent, selecting the object reinforced 60 per cent of the time in preference to the object reinforced 40 per cent of the time. Performance changes markedly, however, when proportional reinforcements closer than 60:40 per cent are used, and the animals give less clear-cut demonstration of such discrimination.

Collectively, these data suggest that some point close to 20 per cent reinforcement represents a threshold value for maintenance of optimal performance. Little, if any, increase in level of performance is obtained with more frequent reinforcement; whereas, with less frequent reinforcement performance deteriorates rapidly.

The drop in latency at 90 per cent may have resulted from a sampling error in the random sequence selections for each animal, since this reinforcement condition occurred seven times in the first half of the experiment in contrast to the next highest frequency of occurrence of five times for the 50 per cent reinforcement condition.

The finding of a significant change in the Blocks within Days effect suggests that satiation, work decrement, or some undetermined process impairs performance within a test day. This process is not normally apparent when such measures of performance as frequency of correct responses are used, although the amount of reward and number of trials may be the same (3).

Brogden (2) has reported a study in which the conditioned flexion response of dogs was reconditioned after extinction by presenting the unconditioned stimulus at some locus other than that used in the initial stages of conditioning. No significant differences were found in the number of test periods needed to recondition to the criterion of 100 per cent conditioned responses for shock applied to the left hind limb, right foreleg, left foreleg (control group), or right thorax. The functional equivalence of shock at loci other than the left forelimb in reconditioning and maintaining left forelimb flexion was designated *incentive generalization*.

The results of the present study provide another example of the Brogden incentive generalization function. In these experiments the stimulus was changed along a dimension of frequency, whereas in the Brogden study the stimulus was changed along a spatial dimension. As the frequency of the reward decreases, the response level remains essentially the same until a critical point located below 20 per cent is reached, at which point the latency begins to increase rapidly. Collectively, the data might be thought of as suggestive of the lower limits of reinforcement necessary for maintenance of optimal performance of a simple instrumental conditioned response.

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[4] Meyer, D. R. Personal communication.

SUMMARY

The effects of fixed-ratio random reinforcement on the latency of an object-displacing response were studied using rhesus monkeys as *S*s. In the initial experiment latency of response was determined for each of 11 conditions of reinforcement ranging from 0 to 100 per cent in 10 per cent increments. The function obtained by plotting mean log latency of response against percentage of reinforcement indicated that latency decreased rapidly as frequency of reinforcement increased to 20 per cent but that the function remained at essentially the same level from 20 to 100 per cent with the one exception that at 90 per cent a significant drop in latency occurred. Significant differences were obtained among the blocks of trials within test days and also among the animals used in the experiment.

The second experiment was designed to locate more precisely the point of inflection found in the latency function of the first experiment by studying the effects on response latency of six reinforcement ratios ranging from 5 to 30 per cent in 5 per cent increments. No significant differences were found between 5 and 10 per cent or 20, 25, and 30 per cent, but between 10 and 20 per cent the latency decreased rapidly and significantly as the frequency of reinforcement increased. Significant differences were found between blocks of trials within days and also between animals as in the first experiment.

The results of the two experiments constitute a demonstration of an incentive generalization function obtained when frequency of reinforcement is experimentally manipulated. The reinforcement function remains at essentially the same level as the degree of similarity of the reinforcement pattern decreases to the 20 per cent ratio, where a gradient becomes manifest with latency increasing markedly as frequency of reinforcement decreases.

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THE EFFECTS OF REPEATED DEPRIVATION EXPERIENCE ON FEEDING BEHAVIOR[1]

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For most animals it is generally assumed that the amount of food ingested and the rate of eating are simple functions of the time and amount of food deprivation (5, 8, 9). In view of the practical and theoretical importance of this premise it is somewhat surprising to find this assumption has little empirical or experimental support. Several recent findings (3, 4, 7) suggest that prior feeding experience is as important a regulator of the amount and rate of intake as any momentary depletion of the nutrient reserve. In addition, Keys *et al.* (6) have called attention to the fact that most animal studies of food deprivation have been short-term investigations concerned either with acute starvation or with specific dietary deficiencies. As far as the author is aware, no systematic, longitudinal study of the food-deprived albino rat has been undertaken.

Accordingly, this experiment sought to furnish empirical answers to the following questions: (*a*) When the albino rat undergoes repeated deprivation, to what extent does the amount and rate of food consumption reflect the amount of deprivation and the consequent physiological need? (*b*) Does the animal change or adjust its feeding behavior when food deprivation is systematically repeated?

METHOD

The *S*s were 64 experimentally naive, albino rats from the colony maintained by the Stanford psychology department. Their ages ranged from 60 to 90 days at the start of the experiment. Initially, the experiment began with only 50 animals. While adjusting to the deprivation schedules, 14 of the original group succumbed. New *S*s of the same age, sex, and prior adaptation training were then substituted.

The original group of 50 *S*s was divided into five groups of ten animals, with the groups equated as to age, sex, and weight. The *S*s were housed in individual living cages with social cues eliminated. Each cage was fitted with a detachable food box at one end and a water bottle at the other. A hinged, aluminum door, opening from the inside of the cage, allowed entrance to the food box. Lever-arm microswitches mounted above each door closed a circuit at each opening. The food boxes were set slightly below the floor level of the cage so that the rat had to withdraw from the food box before eating. Food consisted of Purina Dog Chow so processed that ten pellets of standard size weighed 1 gm.

Records of the feeding behavior were made by an Esterline-Angus ink recorder so situated as to make the sound of its operation negligible. Samples of four 24-hr. records from each experimental group were obtained daily, and individual sampling from each group was systematically varied each day.

The experiment was conducted in a large room in which uniform illumination was maintained both day and night for the entire course of the experiment. Low temperatures were prevented by electric heaters thermostatically regulated to maintain a minimal room temperature of 80° F.

On the initial day each *S* was placed in an individual living cage and provided with water and 30 gm. of Purina Chow in the prepared form. The hinged door of each cage was raised and fixed, allowing *S* unobstructed access to the food. In this experimental arrangement, the *S*s were able to procure and eat only one pellet at a time. Since the wire mesh of the floor of the cage was larger than the pellets, hoarding was prevented. If it dropped a pellet, *S* could not retrieve it. This necessitated the placing of small pans beneath the cage floors in order to determine the number of unconsumed pellets.

After four days of this adaptation, the hinged doors were lowered and the *S*s were required to push open the door in order to feed. These conditions were maintained for ten days. During this period food and water were administered ad libitum.

Following the adaptation period, ten *S*s were randomly assigned to each of five groups. Four groups were placed on 12-hr., 24-hr., 36-hr., and random (i.e., the *S*s were deprived for either 12, 24, or 36 hr. with the deprivation periods altered in random fashion from day to day) periods of deprivation. The fifth group, serving as a control, was fed ad libitum throughout the course of the experiment.

After the appropriate period of deprivation, the *S*s of each of the four deprivation groups were given 20 gm. (200 pellets) of the prepared Purina. At each feeding the 12-hr. group was permitted to eat for 40 min.; the 24-hr. group, for 80 min.; the 36-hr. group, for 120 min.; and the randomly deprived group, for a period equivalent to 40 min. for each 12 hr. of deprivation. These deprivation and feeding schedules were maintained for a total of 40 days. During this period water was administered ad libitum.

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[1] This paper is adapted from a thesis presented to the Department of Psychology of Stanford University in partial fulfilment of the Ph.D. degree. I am indebted to Drs. D. H. Lawrence and Calvin P. Stone for their advice and criticism in the experiment reported here. I am also indebted to the Nutrition Foundation of New York, N. Y., for financial support.

[2] Now at Human Research Unit No. 1, HumRRO, The Armored Center, Fort Knox, Kentucky.

Throughout the adaptation and experimental periods measures were taken daily of the amount of food consumed and of changes in body weight. Food for each *S* was weighed prior to each feeding and again after the remains and spillage had been collected at the end of the feeding period. Rate of consumption and activity evinced toward the food box were measured by means of the Esterline-Angus records. Four *S*s from each of the five groups were recorded daily. Different *S*s were measured each day, and each *S* was measured equally often throughout the experiment.

During ad libitum feeding a feeding session was arbitrarily defined as follows: If at least three openings occurred, separated by no more than 5 min. between openings, a feeding was scored. If at least 15 min. elapsed between a group of three or more openings, two feeding periods were scored.

RESULTS

On the day prior to the introduction of the deprivation schedules the average weight of the 50 animals was 133.8 gm. During the next 40 days, the ad libitum group gained an average of 35 gm. at an approximately linear rate. The 12- and 24-hr. groups lost an average of 12 gm. during the first three days of deprivation training but slowly gained until they each averaged 135 gm. on the fortieth day. The 36-hr. and the random group continued to lose weight until the eighteenth day, when they averaged 100 gm. For the remainder of the experimental period their weight was maintained at this approximate level.

During the last ten days of the adaptation period, when all animals were on ad libitum feeding, no statistically significant differences in food consumption for the five groups were found. The animals averaged 11.9 gm. daily. A comparison of the mean number of feeding sessions per 24 hr., as well as the mean amount consumed each feeding session, also failed to reveal any statistically significant differences between groups.

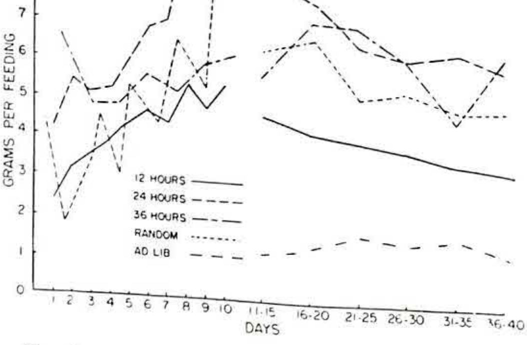

FIG. 1. Average amount of food consumed per feeding. The data are based on the records of the sample of four animals from each group that was recorded on a given day. The data for the 12-hr. group are an average of two feedings.

TABLE 1

Comparison of the Deprivation Groups for the 40-Day Experimental Period

Group	Food Intake in Grams		Time Spent Eating in Min. Per Session	Average Rate of Eating Pellets Per Min.
	Per Session	Per Day		
Ad Libitum	(1.62)	12.92	(11.1)	(1.53)
12-hr.	3.91	7.83	32.1	1.33
24-hr.	6.53	6.53	63.7	1.08
36-hr.	5.87	3.91	84.3	.85
Random			65.2	1.12
12-hr.	5.74		32.4	1.19
24-hr.	4.90	5.27	70.1	1.18
36-hr.	5.18		93.2	.98

Note.—These data are based on the kymograph records for various samples of four animals from each group that were recorded daily. See text for the definition of a feeding session in the case of the ad libitum group.

Although it was initially assumed that the *S*s would feed in a cyclical fashion, no feeding rhythms were in evidence during the adaptation period. Aperiodic feeding characterized all individual *S*s in all of the groups. This aperiodicity has been discussed in detail elsewhere (1). Further substantiation of the aperiodic nature of feeding behavior was obtained from the behavior of the ad libitum group during the experimental period. No evidence for rhythmicity in feeding or for the gradual development of feeding cycles was obtained.

With the introduction of the deprivation schedules, a gradual change in eating behavior was observed for all groups during the first ten days. During this period all the experimental groups gradually increased the average amount of food consumed at each feeding session. These trends are shown in Figure 1. During the last 30 days, following the stabilization of food intake, the *S*s of the 24-hr. group averaged the highest intake per session. They were followed, in order, by the 36-hr., the random, and the 12-hr. groups. The mean values for all groups are shown in Table 1. While the mean

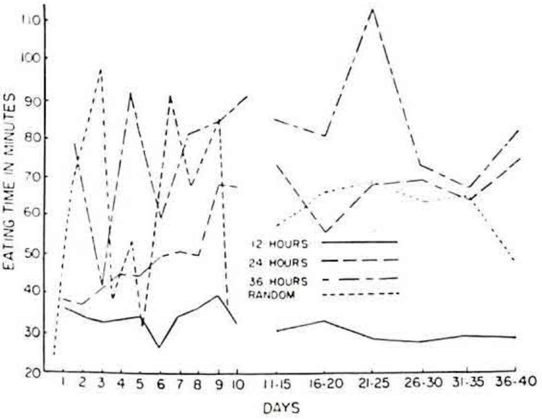

FIG. 2. Average elapsed time in minutes when feeding ceased. This was measured from the moment food was made available to the time at which the animal made no further returns to the food box. The data are based on the records of the sample of four animals from each group that was recorded on a given day. The data for the 12-hr. groups are an average of two feedings.

value for the ad libitum group is also included, it should be noted that for this group a feeding session was defined on a different basis. Thus the results for this group are not strictly comparable to the others.

An analysis of variance (2) based on the means of the four experimental groups indicated the differences were significant well beyond the .01 level. A comparison of the average amounts consumed by the random group following the various deprivation intervals, however, revealed the greatest consumption after 12 hr. and the least after 24 hr. of deprivation. An analysis of variance based on these three means indicated that the differences were only significant between the .05 and .10 levels. When the amount consumed *per day*, rather than per session, is considered, it is apparent from Table 1 that a perfect negative correlation between the length of deprivation and the intake existed for the experimental groups.

Corresponding to the changes in intake at each session, Figure 2 indicates there were also changes in the amount of time spent in feeding. The elapsed time spent in eating was measured from the moment food was made available to the animal to the point in the session where no further return to the food box was indicated by the kymograph record.

During the first few days of the experimental period, most of the animals in the 12-hr. group ate during the entire 40 min. that food was available. For the remainder of the 40 days, however, the average time spent in feeding gradually decreased. By the end of this period no animal spent all the available time in feeding. In the early stages of the deprivation training the *S*s of the 24-hr. group ate for only half of the 80 min. provided. As the deprivation was repeated, however, the time spent in feeding increased until the majority of the *S*s ate for the entire period during the last 20 days of the experiment. The behavior of the animals in the 36-hr. group, as indicated by this measure, exhibited large variations from session to session. Nevertheless, a tendency for the *S*s to increase their eating time gradually during the first 20 days and then to decrease it was indicated. With the exception of one or two sessions in the middle of the experimental period, animals in this group rarely spent the entire 120 min. in eating, or in opening the food boxes. While not apparent from the limited data given in Figure 2, the three trends mentioned above were also noted in the random group for the various deprivation intervals. The mean time spent in eating, averaged over the entire 40-day period, is shown for each group in Table 1.

In order to show the relationship between the amount consumed and the time spent in eating, the rate of food intake was defined as

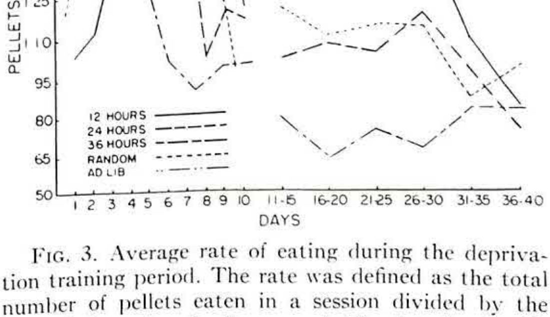

FIG. 3. Average rate of eating during the deprivation training period. The rate was defined as the total number of pellets eaten in a session divided by the elapsed time when feeding ceased. The data for the 12-hr. group are an average of two feedings.

the number of pellets eaten per session divided by the total time spent in feeding. Total feeding time was regarded as the number of minutes elapsing between the onset of feeding and the time after which the animal failed to return to the food box. This rate was computed separately for each animal and the individual rates averaged to produce the curves in Figure 3. Since a feeding session for the ad libitum group was defined differently, it should be noted their rate measures are not strictly comparable to the others. The mean rate of consumption over the 40-day period for each group is shown in Table 1. The perfect negative correlation between the length of deprivation and the rate for the 12-, 24-, and 36-hr. groups is readily apparent. An analysis of variance performed on the rate differences between these three means indicated the differences to be significant well beyond the .01 level. The fact that the animals ate only a moderate amount each session and consumed it rather slowly was responsible for the low-rate value for the 36-hr. group. For the 12-hr. group, the relatively high rate resulted from the food being consumed in a rapid fashion. In the random group the same negative relationship between deprivation time and rate was found. The difference between the 12- and 24-hr. intervals, however, was not as marked.

While it was originally assumed that the amount of activity displayed toward the food boxes between feedings would parallel the length of the deprivation interval, no such relationship was found. Although no statistically significant differences were obtained, in the initial stages of training the 24-hr. group averaged more such activity than the other groups. For all groups a general reduction in this activity occurred as the deprivation experience was continued.

DISCUSSION

From these data it is clear that the adjustment to a deprivation cycle is a gradual process marked by continuous changes in eating behavior during the first ten days. This is most apparent in the increase in total intake per feeding period shown by each of the four experimental groups. It is also apparent in the increase in total time spent in eating per feeding period. Although this latter increase is not shown by the 12-hr. group, it may well be because food was available for only 40 min. at a time. The existence of such marked changes in feeding behavior would seem to have several implications for motivational theory. First, any attempt to establish a simple relationship between length of deprivation and strength of drive, where drive is measured by feeding behavior, would hold only for animals already adapted to a definite feeding rhythm.

Second, the fact that all the experimental animals, other than those of the 36-hr. group, doubled their intake per session during the first ten days of deprivation raises the question of why the animals stopped eating so soon during the first few deprivation periods. The more orthodox conceptions of "physiological need" seem rather inadequate when it is realized that *S*s of the 12- and 24-hr. groups showed no loss of weight after the third day. Their intake, however, continued to increase. On the other hand, *S*s of the random and 36-hr. group continued to lose weight until the eighteenth day, approximately at the point of their maximum intake. Nevertheless, for the 36-hr. group the actual increase in average intake during this period was relatively small when compared with the amount consumed by the random group. The mere fact that the groups doubled their intake during the first ten days, despite some weight loss, should also be noted. This fact makes rather improbable any assumption that the initial inhibition of eating was due to any physical limitation such as stomach capacity. Instead, the behavior changes in rate and feeding time observed to accompany the increased consumption suggest that the initial inhibition of eating was due to previous habits established during ad libitum feeding. These habits had to be modified before the animal could show any compensatory eating. One would normally expect such a process to be relatively slow and continuous. Even if this interpretation were correct, the failure of the animals to show complete compensation remains to be explained. None of the animals returned to the pre-experimental level of intake even though food was available to them for longer periods than they actually spent in eating.

Although the 12- and the 24-hr. groups had similar weight curves, the 12-hr. group ate significantly more per day than the 24-hr. group. Similarly, the weight curves for the 36-hr. and the random groups were almost identical throughout the 40 days. The random group, however, ate significantly more per day on the average than did the 36-hr. group. These comparisons, revealing differential daily intake in spite of similar changes in weight, suggest that (*a*) the type of scheduling of the eating periods results in differential efficiency in the digestion and use of the food material, or (*b*) along with the changes in eating behavior there are corresponding changes in the expenditure of energy through activity, heat loss, and the like. Some evidence (7) exists to favor the latter alternative. If such changes do occur, then complete compensatory eating is not to be expected since changes in the expenditure of energy will reduce the demand for food.

Irrespective of the deprivation schedule imposed, all the experimental animals had access to food for the same amount of time each day. Nevertheless, a perfect negative correlation between the mean intake of food *per day* and the length of the deprivation interval was found. This relationship is somewhat complicated by the differential weight loss of the 36-hr. group, as compared with the 12- and 24-hr. groups. In the case of the latter groups, however, with exactly the same weight curves throughout the experiment, the 12-hr. group ate significantly more per day than did the 24-hr. group. The relationship between length of deprivation and intake is further complicated by the behavior of the random group. For these animals only minor fluctuations in weight from day to day were correlated with the length of the preceding deprivation period. Nevertheless, their average intake *per feeding session* was greatest after 12 hr. of deprivation, next greatest after 36 hr., and least after 24 hr. This was a very different order from that obtained for the three experimental groups on a constant deprivation schedule. If the deprivation experience were continued, the possibility exists that intake per session would become totally independent of the length of the immediately preceding deprivation interval. If further studies support this possibility, stronger evidence would be afforded for the hypothesis that any relationship between deprivation interval and intake is found only when a definite feeding rhythm is well established.

Because of the arbitrary definition of a feeding session, interpretations of the data on rate of eating are seriously limited. These data, however, suggest at least one interesting behavioral contrast. It was noted that the ad libitum animals ate small amounts at frequent intervals. All their feeding, however, occurred at a relatively high rate. When increasing lengths of deprivation were imposed on the other *S*s, the average daily intake decreased but the length of time spent in eating increased. For the 36- and 24-hr. groups a marked reduction in rate of food intake was noted. This behavior is remarkably similar to the behavior of human *S*s noted by Keys *et al.* (6). They reported that semistarved men would dawdle for two hours or more over meals they previously had consumed in 20 min.

SUMMARY

Changes in the feeding behavior of animals placed on various deprivation schedules were measured over a 40-day interval. Five groups of rats, ten animals to a group, were used. Three groups were placed on either a 12-, 24-, or 36-hr. deprivation cycle; the fourth, the random group, experienced all three deprivation intervals but in random order; the fifth group served as a control and was fed ad libitum. Measures were taken of the food intake, time spent in eating, activity shown toward the food container during deprivation intervals, and body weight. The results were as follows:

1. During the first 10 days a relatively slow adaptation to the deprivation schedule was shown by all the experimental groups. With the exception of the 36-hr. *S*s, all the experimental groups doubled their intake per feeding during the first ten days. With the exception of the 12-hr. group, all the experimental groups spent more time each session in eating. For the experimental groups, however, no consistent relationship between the amount eaten and the time spent in feeding was noted.

2. In terms of daily intake of food, there was a perfect negative correlation between length of deprivation and food consumption. This relationship was also noted for the various deprivation intervals in the random group.

This could not be accounted for in terms of differential weight loss.

The results suggest that (*a*) any direct relation between the length of a deprivation interval and feeding behavior is largely the result of having previously established a definite feeding rhythm, and (*b*) the adjustment to any imposed feeding schedule is accompanied by a radical modification of past eating habits and of behaviors controlling energy expenditure.

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INTAKE AND WEIGHT ADJUSTMENTS IN RATS TO CHANGES IN FEEDING SCHEDULE[1]

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A common technique in the study of hunger-motivated behavior in animals is to place them on deprivation schedules with food available for only a limited time each day. Frequently in such studies the deprivation interval is lengthened or shortened at some critical test phase of the experiment. It has been noted that *S*s' adjustment to these shifts in schedule is relatively slow as indicated by changes in daily food intake (2, 3). This has led to the suggestion that part of this adjustment depends upon learning; the sudden shift in deprivation time brings into play internal and external cues that have not previously been associated with eating behavior (1, 2, 4). One implication of this hypothesis is that with repeated experience with these shifts in deprivation time, the adjustment period should decrease as the result of transfer. There appears, however, to be relatively little systematic data concerning the rapidity of these adjustments, their influence on food-seeking behavior, or on changes in rate of these adjustments with repeated experience of this type.

In conjunction with another study, the present authors had occasion to place a group of 34 albino rats on a 22-hr. deprivation schedule for a period of 61 days during which systematic records of food intake and weight were made. The *S*s were then returned to a free-feeding schedule for two weeks and then once again placed on a 22-hr. deprivation schedule. Two things were noted from the intake records: (*a*) *S*s not only showed the usual relatively slow adjustment to the deprivation schedule but also a tendency to "overeat" when returned to the free-feeding schedule. Finger and Reid (3) also noted this tendency. (*b*) There was some indication that the second adjustment to the 22-hr. deprivation schedule was more rapid than the first. This was in keeping with the hypothesis that learning played a part in these adjustments. With these tendencies in mind, subgroups of the *S*s were continued on successive periods of 22-hr. deprivation with intervening periods of free feeding until they had completed five such cycles of deprivation and recovery. This paper summarizes the results in terms of daily intake and weight changes.

METHOD

The *S*s were 34 albino rats, half of which were males and half females, between 60 and 90 days of age at the beginning of the study. They were adapted for a two-week period to individual living cages in a room where the minimum temperature was set at 76° F. During this period water and food were continuously available. The food throughout the study consisted of small-sized "Friskies." All *S*s were then placed on 22-hr. deprivation schedule for 61 days, returned to free feeding for 14 days, and then again placed on a 22-hr. deprivation schedule for 14 days. During the first deprivation interval, daily intake records were made, with allowance for spillage, and *S*s weighed once a week. Starting with the first day of the recovery or free-feeding period and for the remainder of the study, daily intake records were made and *S*s weighed every other day. These records were made at the same time each day throughout the study.

At the end of the second 22-hr. deprivation period, day 88, *S*s were divided into three groups equalized on the basis of average weight and intake for the previous week. The nine *S*s in group A were placed on ad libitum feeding, with food continuously available for the remainder of the study. The 17 *S*s in group B were placed on ad libitum feeding for 14 days, returned to a 22-hr. deprivation schedule for 14 days, and so on, until they had completed an additional 7 of these two-week periods. The eight *S*s in group C continued on the 22-hr. deprivation schedule for 12 additional weeks and then on day 172 were shifted to ad libitum feeding for the remaining two weeks. These relationships of ad libitum feeding and deprivation schedules are best shown in Figure 2.

RESULTS

The food intake curves during the 22-hr. deprivation periods are shown in the left panel of Figure 1. Curve 1 is based on records of all 34 *S*s in their first deprivation period (days 0 to 13); curve 2 on all 34 *S*s in their second deprivation period (days 74 to 88). Curves 3, 4, and 5 are based on the three successive 22-hr. deprivation periods of group B which occurred on days 102 to 116, 130 to 144, and 158 to 172, respectively. On the day prior to the first dep-

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[1] This study was supported in part by a research grant from the Nutrition Foundation of New York.

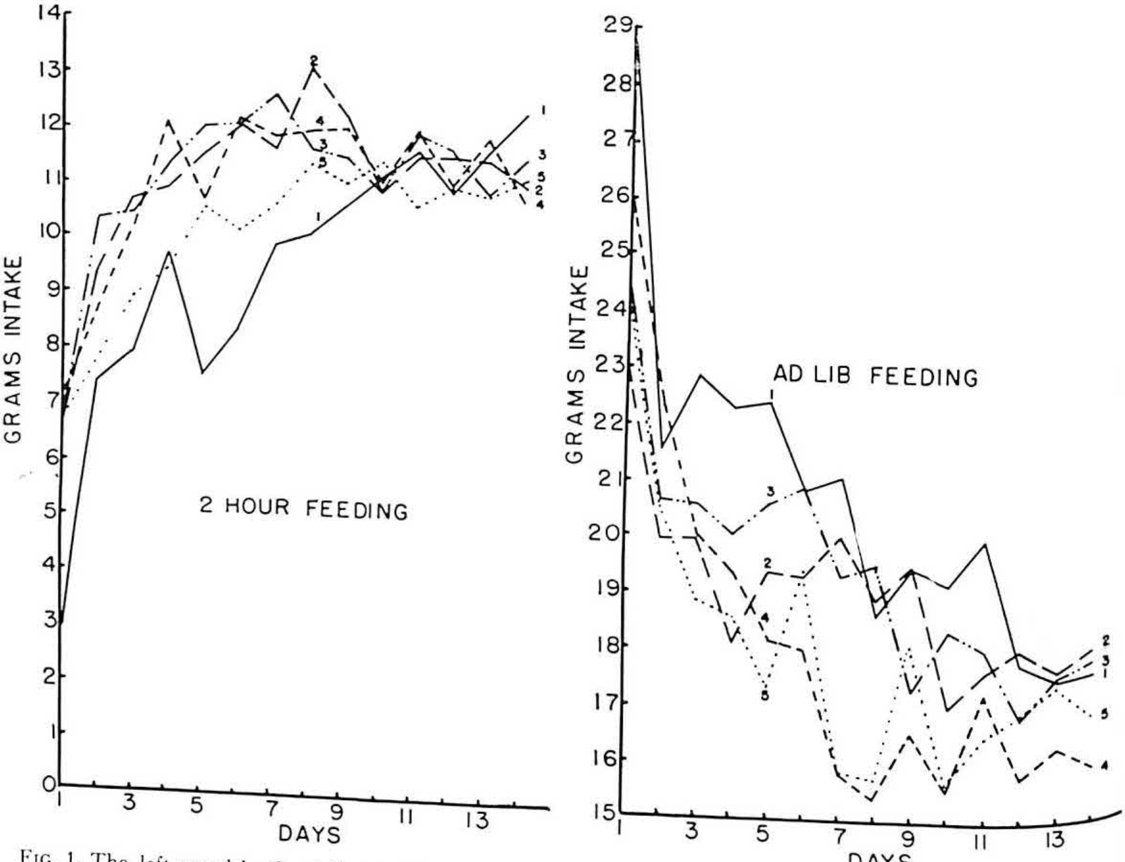

FIG. 1. The left panel is the daily food intake for five successive periods of 14 days each when *S*s were on a 22-hr. deprivation schedule. The right panel is the daily food intake of the same *S*s for five successive periods of 14 days each when they were returned to a free-feeding situation.

rivation experience *S*s' food intake averaged 18.6 gm. It is apparent that in each instance there is a marked reduction on the first day of deprivation, with only a gradual increase over the next five to seven days to an asymptote. During the deprivation periods of group B, represented by curves 3, 4, and 5, *S*s in group C, which were also on a 22-hr. deprivation schedule, averaged between 10 and 12 gm. per day. There is a suggestion that the first adjustment to this deprivation schedule, curve 1, occurred more slowly than later ones. However, there is no apparent differentiation between the remaining four curves. The depression of curve 5 is probably due to the fact that during this time the room temperature rose above 90° on several days just about the time *S*s were feeding.

The right panel of Figure 1 shows *S*s' adjustment to the ad lib. feeding situation. Curve 1 is based on the first recovery period for all 34 *S*s; the remaining curves are the four successive recovery periods for the 17 *S*s of group B. During the successive periods represented by curves 3, 4, and 5, the *S*s of group A, which were also on ad libitum feeding, averaged between 17 and 18.5 gm. per day. By comparison it is apparent that there is a marked tendency for *S*s to "overeat" for the first five to seven days when returned to the ad lib. situation after a period of deprivation experience. Again there is a suggestion that the first of these adjustments during a recovery period occurred somewhat more slowly than in later recovery periods, but this difference is by no means marked.

The weight curves for the various groups are shown in Figure 2. These tend to mirror the intake curves, falling off when *S*s are placed on deprivation and increasing rapidly when they are returned to free feeding. But it should be noted that the weight curve for group B tends

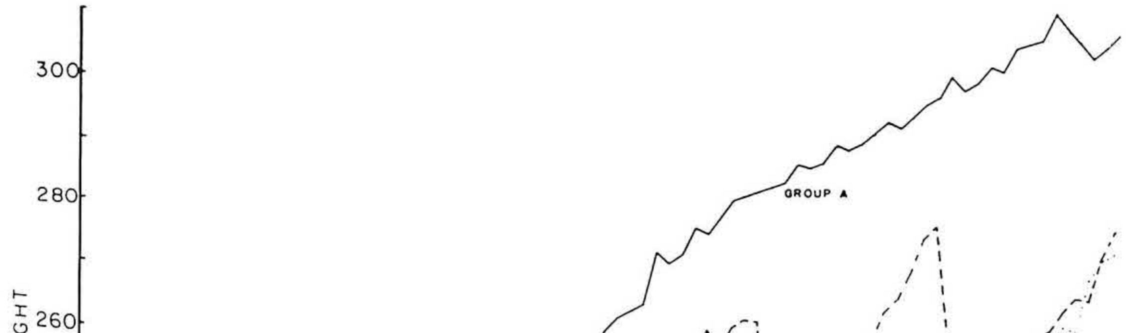

FIG. 2. The solid line for the first 87 days is based on the average weight for all 34 *S*s. During the first 60 days weights were taken only once a week. Starting with day 61, they were taken every second day. Consequently the actual day of shift from a deprivation to a free-feeding period, and conversely, is accurately represented by the vertical lines on the bottom third of the graph.

to remain between the curves for groups A and C; the food intake for group B, under both deprivation and ad libitum conditions, tends to level off considerably before the average weight in this group has reached that of the corresponding control group.

DISCUSSION AND SUMMARY

This study has recorded the adjustments in food intake and weight that occurred when subgroups of 34 albino rats were repeatedly shifted from ad lib. feeding to a 22-hr. deprivation schedule and conversely. The results indicate that when these *S*s are shifted from the ad libitum feeding to the 22-hr. deprivation schedule, there is a seven- to ten-day period during which *S*s gradually increase their intake. Meanwhile their weight decreases. When these *S*s are returned to ad libitum feeding, there is a comparable period of readjustment during which they "overeat" with a gradual decrease in intake to a new level. There is a corresponding acceleration in their weight.

These data also suggest that the first of these adjustments, either from the ad libitum to the deprivation condition or conversely, occurs more slowly than do later ones. This tends to be in keeping with the hypothesis that these adjustments represent in part a period of learning to eat in response to the changed internal and external cues. However, there is no clear evidence that this increase in the rate of adjustment continues with repeated experiences of this type. But as a test of the learning hypothesis, these data are contaminated by the fact that *S*s were continually increasing in average weight. If the rate of adjustment is a joint function of physiological factors, such as those mirrored by changes in weight, and learning, the influence of the latter would be obscured by the progressive change in weight.

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THE EFFECT OF ADRENOCORTICOTROPHIC HORMONE (ACTH) ON AVOIDANCE CONDITIONING IN THE RAT[1]

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The various changes in mood and behavior that may occur in patients treated with adrenocorticotrophic hormone (1, 6) have made it pertinent to assess the effect of exogenous ACTH on behavior motivated by noxious stimulation. That some effect of ACTH on avoidance conditioning does occur is revealed in studies discussed by Mirsky, Miller, and Stein (5).

In avoidance conditioning the animal must respond appropriately to the conditioned stimulus in order to prevent the occurrence of the painful unconditioned stimulus. Consequently, it may be postulated that any modification of the response to a noxious stimulus would be reflected in avoidance conditioning.

METHOD

Subjects

Thirty-one male Wistar rats 100 to 120 days old were used. The *S*s were maintained on an ad libitum supply of food and water throughout the experiment. The animals were randomly assigned to the experimental conditions.

Apparatus

The tests were conducted in a two-compartment apparatus. The unit was 23 in. long, 7 in. wide, and 9 in. high. A 2-in. barrier of stainless steel bars 1/8 in. in diameter, 1/2 in. apart, separated the two compartments. The top bar of the barrier was mounted on bearings to prevent perching. The floor was a grid of stainless steel rods identical in size and spacing to those described for the barrier. The two ends and the top were made of wood, and painted white inside. One side consisted of a sheet of white milk glass. Illumination was provided by two 25-w. bulbs located behind this translucent glass. The remaining side consisted of two pieces of plain glass with a black cloth inserted between them. This made it possible to observe the animal without the distraction of movements by *E*.

A push-button switch activated a buzzer and a time-delay relay that automatically delivered a shock to the animal after 5 sec. if it failed to respond (110 v. with 85,000 ohms in series with the animal). Another push-button switch made it possible to terminate the buzzer, or buzzer and shock, when the animal performed the response. A pilot light connected in parallel with the shock circuit made it possible to define the response as conditioned or unconditioned. The desired response consisted of moving across the barrier to the other compartment.

Procedure

After a 2-min. adaptation period, the conditioned stimulus was presented. The unconditioned shock stimulus was presented after 5 sec. if the animal failed to respond to the buzzer. The buzzer, or buzzer and shock, were terminated when the animal responded. The daily test period consisted of 15 such presentations at regular 60-sec. intervals. The animals were run on consecutive days.

Throughout the conditioning phase, half the animals were given a daily subcutaneous injection of 5 mgm. of ACTH suspended in a gelatin vehicle. The remaining animals received equivalent injections of the gelatin vehicle.

After attaining the conditioning criterion, the groups were again divided and extinction was started. Half the group which had received ACTH was given gelatin while the remainder of this group was given ACTH throughout extinction. Similarly, half the animals conditioned with the control gelatin were given ACTH, and the remaining animals were given gelatin during the extinction phase (Table 1). The injections were administered approximately 90 min. before the daily test period.

The criterion of conditioning was arbitrarily set at the 80 per cent level for one test period with not more than one failure to respond in the last ten trials. The criterion of extinction was failure to respond at or above the 20 per cent level with not more than one response in the last ten trials. During extinction the buzzer was terminated manually after 5 sec. if the animal failed to respond. As is customary, the unconditioned shock stimulus was omitted throughout extinction.

In an additional experiment 23 male, Wistar rats, 100 to 120 days old, were used. The above procedure was employed except that the animals were injected only in the conditioning phase and the criteria of conditioning and extinction were arbitrarily doubled in an attempt to secure more normally distributed extinction scores. For example, the criterion of conditioning was 80 per cent response for two consecutive days with not more than one failure to respond in the last ten trials of a criterial test period.

RESULTS

The 15 animals treated with ACTH required 91.0 mean trials to attain the criterion

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[2] The authors are indebted to Dr. I. Arthur Mirsky for suggestions and criticisms and to the Armour Company for generous supplies of Acthar.

of conditioning as compared with 74.0 mean trials for the control animals. This difference, as well as the difference between groups in number of conditioned responses to criterion, was insignificant with the *t* test.

Group extinction data are summarized in Table 1. Examination of the data revealed the exponential nature of the distribution with a piling up of zero responses in extinction. Consequently, the Festinger test (2), devised specifically for this type of distribution, was used in place of the customary *t* test in the analysis proposed by Lindquist (4, p. 22). A significant interaction was found between the four conditions. Additional analysis indicated that the animals treated with ACTH during the conditioning period responded significantly longer ($p = .01$) in extinction than the animals that were given the gelatin vehicle. There was no significant difference between the effect of ACTH and the gelatin vehicle administered during extinction.

The factorial design (Table 1) suggested that the extinction rate of animals that were conditioned while receiving ACTH was significantly prolonged over that of animals conditioned while receiving the gelatin vehicle. This suggestion was tested in an additional experiment, the data of which are summarized in Table 2. It is apparent that no significant differences occurred in the conditioning phase. Arbitrarily doubling the criterion did not serve to normalize the extinction scores; consequently, the extinction data were evaluated with the Festinger test (2). (There were four animals in the ACTH group with zero respones in extinction as compared with four such scores in the control group.) The animals receiving exogenous ACTH throughout the conditioning phase required a longer time to extinguish the response. This difference was significant beyond the .01 level.

TABLE 1

Number of Conditioned Responses in Extinction with the Hormone-Nonhormone Condition Indicated

Conditioning Treatment	Extinction Treatment			
	ACTH		Gelatin	
	No. of Animals	Mean	No. of Animals	Mean
ACTH ($N = 15$)	7	16.85	8	16.5
Gelatin ($N = 16$)	8	4.5	8	8.89

TABLE 2

Comparison of Conditioned Responses and Trials to Criterion

Phase and Group	N	Mean Conditioned Responses	p	Mean Trials	p
Conditioning					
Untreated	11	53.18		88.64	
Treated	12	44.75	.11	85.	
Extinction					
Untreated	11	27.09		84.54	
Treated	12	113.42	.01	197.5	.01

One animal was arbitrarily terminated when failure to extinguish was encountered after 750 trials. Although the data for this animal were included in our statistical analysis, the group differences were significant beyond the .01 level even when this animal was excluded.

DISCUSSION

No significant differences in rate of extinction were found which might be attributed to ACTH administered during extinction. This finding is contrary to preliminary evidence on monkeys discussed by Mirsky, Miller, and Stein (5). Whether this represents a procedural difference, a species difference, or some other variable cannot be answered at the present time.

The acquisition of a conditioned avoidance response was found to be unmodified by exogenous ACTH. There were no significant differences between control and experimental groups in the number of trials to reach the criterion of conditioning, nor in the number of conditioned responses to the conditioning criterion. Further, there were no gross behavioral differences between the animals that received the hormone and the control animals. However, those rats which were treated with ACTH during conditioning subsequently extinguished in a significantly longer period than did the controls.

Additional evidence that the anterior pituitary hormone may be important in the formation of conditioned responses is given by Graham (3). He reports a personal communication from Applezweig, who has found in preliminary investigations that hypophysectomized rats were incapable of forming avoidance responses in a modified Mowrer-Miller shuttlebox. When the hypophysectomized rats were treated with ACTH, they showed some evidence of avoidance learning.

Although it is tempting to interpret the present results in terms of "fear" and possible perceptual changes, insufficient data are available to justify such an interpretation.

SUMMARY

Two experiments were completed in an attempt to assess the effect of ACTH on avoidance conditioning in rats. Although the administration of ACTH during conditioning did not affect the acquisition of the response, it did significantly prolong the subsequent extinction rate.

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VISUAL PATTERN PERCEPTION FOLLOWING SUBPIAL SLICING AND TANTALUM WIRE IMPLANTATIONS IN THE VISUAL CORTEX[1]

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Important integrative roles have been ascribed in theory to the tangential intragriseal irradiation across the cerebral cortex of excitatory effects in the form of discrete nerve impulses and mass direct currents. In an earlier effort to test the possible importance of tangential intracortical conduction, we found that multiple subpial knife cuts extending through the depth of the gray matter and placed in criss-cross patterns throughout the sensorimotor and neighboring cortex of the monkey failed to produce any marked disruption of motor coordination (10). Similar subpial slicing of the exposed striate cortex in the monkey likewise failed to cause any detectable impairment of function in simple tests of visual perception. The performance of control cases with the same cortical area excised proved to be sufficiently good, however, to render this latter finding indecisive. Visual perception in the monkey has been found to survive also an electrical short-circuiting of the exposed portion of the striate cortex with overlaid gold bands and inserted pins (5).

No significant functional role of transcortical conduction either of nerve impulses or of gross direct current has been revealed in the foregoing. However, a final interpretation cannot be reached in the absence of further surgical controls along with more refined functional tests. Definitive experiments with respect to vision in particular are needed because many of our current concepts of cerebral organization are based specifically on phenomena of visual perception (2, 3, 4, 7, 8, 11). Moreover, hypotheses concerning the cerebral mechanisms of visual pattern perception constitute at the present time the most specific formulations available for the neural correlates of subjective experience.

METHOD

Apparatus, Subjects, and General Procedure

Cats, one-half to three-fourths grown at the start, were trained to select an equilateral triangle when paired with various ones of the series of other imperfect triangular patterns of the same dimensions shown in Figure 1. A darkened discrimination box was designed in which the two stimulus figures were presented side by side, 10 cm. apart in two doors at one end of the box. The white translucent stimulus figures illuminated by transmitted light from an outside source stood out distinctly in the dark uncomplicated by frame or border relations. The outer edges of the positive equilateral triangle were 7.5 cm. in length, and the animals made their choice at distances ranging from approximately 10 to 35 cm. By selecting and pushing open the correct door holding the positive figure the cats obtained a morsel of food. A sliding bolt prevented the incorrect door from opening more than 1 cm. When an incorrect

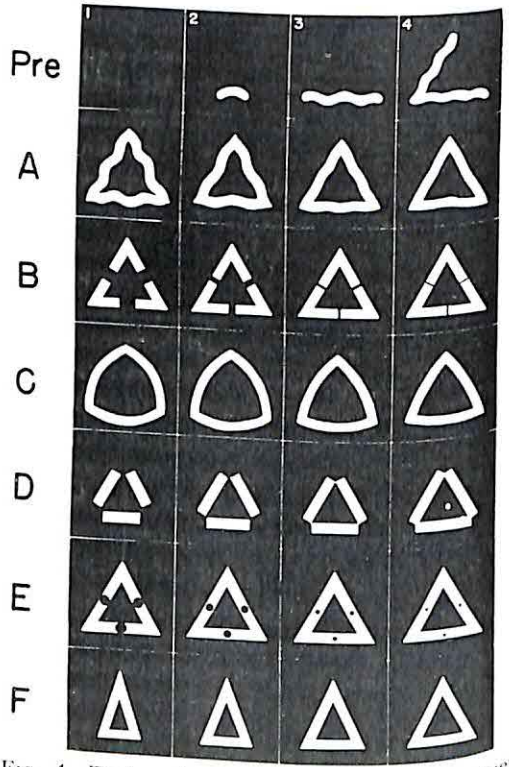

FIG. 1. Test scale of negative figures that were paired individually with the single positive figure which was an equilateral triangle like E4 without the dots (see also Fig. 3A). Training proceeded from left to right, top to bottom, beginning with the preliminary series, *Pre*.

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[2] The major portion of the work was completed while the authors were with the National Institute of Neurological Diseases and Blindness, stationed at the University of Chicago.

choice was made, the cats failed to get food and received mild punishment in the form of abrupt withdrawal from the box, rough handling, and an occasional light slap.

In order to test specifically for possible pattern-disturbing effects of the surgical procedures, the negative stimulus figures were designed in the form of distortions or imperfections of the positive figure. For each pattern type four figures of increasing difficulty were arbitrarily selected to form the 6 series, A to F, of the test scale shown in Figure 1. More difficult discriminations than those of column 4 were possible, but the extra time involved in training and the instability of the more liminal discriminations contraindicated their use for postoperative testing.

Training Program

The regular training schedule involved 20 to 30 trials per day, five to six days per week. Irregularities were common, however, owing particularly to suspension of training while the cats had respiratory and other infections and during interruptions for other experiments. As we were not concerned directly with the learning process or memory capacity as such, considerable individual variation was permitted in the training program.

The cats were trained to a criterion of 17 correct out of 20 consecutive trials on all the negative figures with which they were to be tested after surgery. Approximately 50 training days were required on the average to master the complete series A through F. Surgery was postponed until at least 50, and generally many more, overtraining trials had been run on each of the top figures. During the overtraining period and in all the postoperative tests, the figures were interchanged at random in accordance with Gellerman's (1) principles. Care was also taken during these trials to eliminate the use of accessory cues based on brightness, total flux of light, odor, sound, or on accidental characteristics of individual stimulus cards or of individual trainers.

Operative Procedure

The operations were performed aseptically with the cats under sodium pentobarbital anesthesia (38 mg. per 1 kg. body weight, intraperitoneal). The skull was opened widely on each side and across the midline. The cortical knife cuts were made with subpial knives (10) with cutting blades of 1.9 and 2.1 mm. in depth. The metallic wires inserted in the cortex were cut from surgical sutures of tantalum, B and S gauge No. 30 and No. 33. Tantalum, with an electrical conductivity approximately one-seventh that of copper, was chosen because of its extreme biological inertness. No effort was made to confine the wires to the cortical gray and many of them extended deep into or through the subjacent white matter. Visual cortex both I and II as described by Talbot and Marshall (12) were included in all cases. Excision of the superior colliculi was started with a shallow subpial knife, after which the loose tissue was removed with weak suction. Preliminary removal of the visual cortex on one side or, in other cases (*Mrc* and *Stf*), division of the caudal third of the corpus callosum was involved in removal of the colliculi. The finer aspects of all operations were carried out with the aid of a wide field stereoscopic microscope with a magnification of 7×. A medial bridge of bone 1 to 2 cm. wide was replaced over the sagittal sinus. Procaine penicillin G (300,000 units) was injected intramuscularly at the beginning of the operation and again on each of the next three days.

A minimum of ten days was usually allowed for recovery from the surgery. The top test patterns were then introduced with a preliminary trial on each of the simpler stimulus cards of the same pattern type. If the animal failed to make criterion it was tested on the next easier figure of the series. As a rule, only one negative series was tested on a given day. However, the foregoing general procedure was evolved gradually in the course of the experiments, and exceptions were common especially among the earlier cases.

Finally, following a lethal dose of sodium pentobarbital, the head was perfused post mortem with 10% formalin, and the brain removed. Appropriate records were then made in the form of X rays, photographs, and camera-lucida drawings. The lesions were studied histologically in sections prepared with the Weil myelin, Mallory connective tissue, and cresyl violet Nissl stains.

CASE RECORDS

Subpial Slicing

Case Snt. Left and right superior colliculi and the left visual cortex were removed prior to training. *Snt* was then taught to discriminate between the positive equilateral triangle and the negative figures A3, B3, C3, D4, and E3, in a total of 48 days spread over a period of four and one-half months. This included only 50–70 overtraining trials per figure, and the performance remained comparatively erratic. The remaining (right) visual cortex was thereupon sliced with intersecting knife cuts as illustrated in Figure 2.

The postoperative tests were delayed in this first case by development under the incision of an abscess which drained during the second week after operation and gradually closed during the third. Scores on the postoperative tests conducted over a ten-day period beginning on the 18th day after operation were somewhat below the preoperative level at the beginning on the A3 and B3 figures but by the 28th day, *Snt* had achieved criterion or better on all his top test figures.

On post-mortem examination the knife cuts in the right cortex were found extending through the gray matter in most places and at erratic intervals a short distance into the white matter (cf. Fig. 4). The superior colliculus was

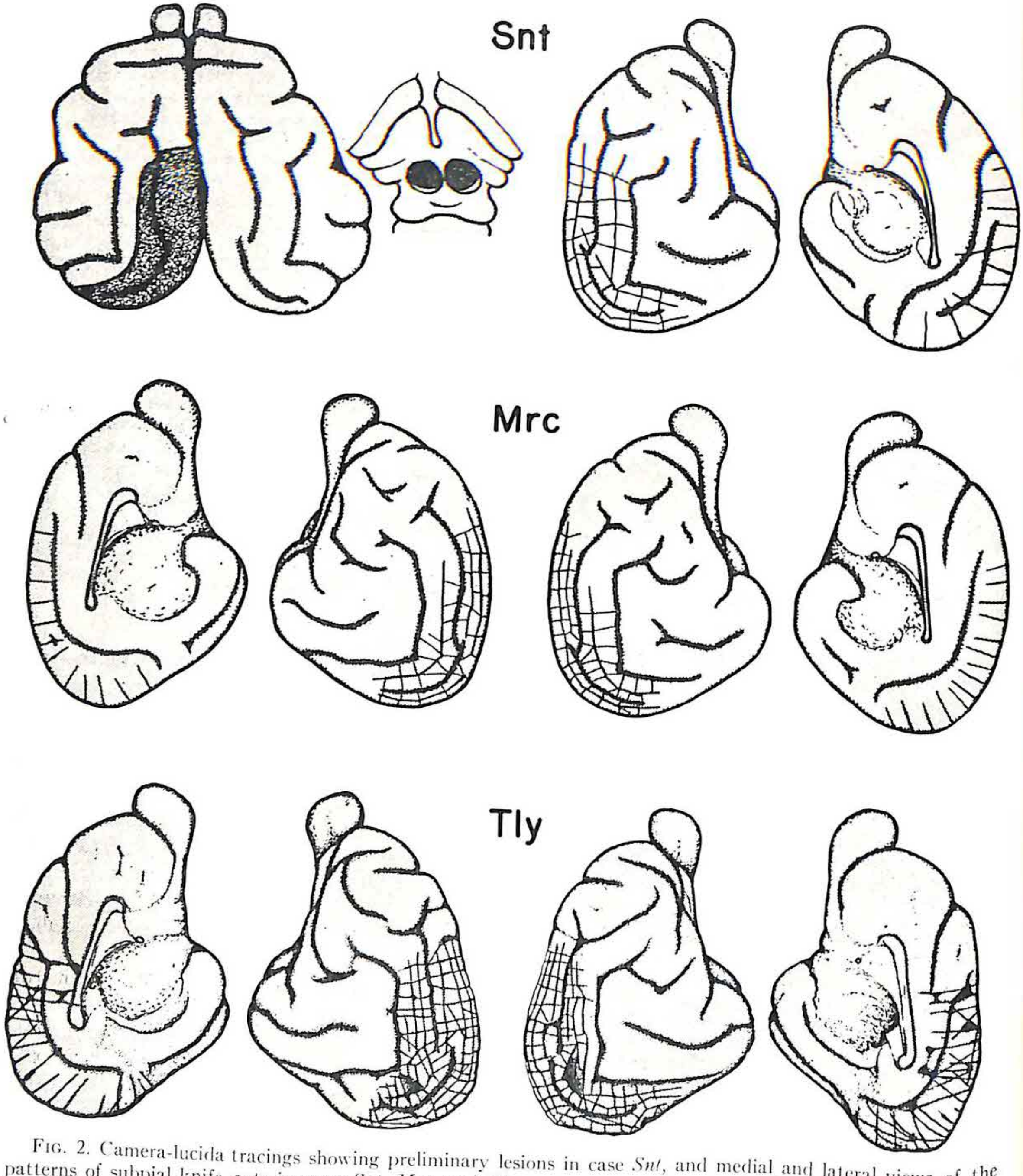

FIG. 2. Camera-lucida tracings showing preliminary lesions in case *Snt*, and medial and lateral views of the patterns of subpial knife cuts in cases *Snt*, *Mrc*, and *Tly*.

missing on the left side except for a small lip at the posterior edge. On the right, the laterocaudal border of the colliculus was intact, but it appeared doubtful that any optic fibers to this area had escaped the lesion.

Case Mrc. This cat was trained to discriminate figures A3, B4, C4, D4, E3, and F3 with 90 to 160 overtraining trials for each figure. The preoperative training required 76 days spread over a period of six months. The visual cortex in both hemispheres was then sliced with multiple subpial knife cuts in the patterns shown in Figure 2.

Beginning on day 11 after operation, *Mrc* ran the first 20 trials on each of the figures A3, C4, D4, and F3 with no errors. Perfect scores were also obtained by day 20 on B4 and E3, but not without a significant number of initial errors (11 and 14 respectively) suggesting some selective effect of the cortical lesions for the B and E patterns.

A second operation six weeks after the first was undertaken to remove the superior colliculi. There was no evidence of vision during the first several days after this operation. Some visual capacity had returned by the end of the second week and testing was resumed. One month after the second operation the highest figures on which criterion had been attained were A2, B2, C1, E1, D4, and F1. The pupils remained widely dilated after the second operation indicating damage to the pretectal nuclei (6). Impairment of the mechanisms for focusing may thus have been a complicating factor. Discrimination even at these lower levels of the test scale, however, indicates a fair capacity for form discrimination comparable at least to that involved in differentiating, for example, a triangle from a circle.

The midbrain lesions invaded the deeper layers of the colliculi as far as the stratum griseum profundum and extended far forward on both sides into the pretectal nuclei. In addition an area of secondary degeneration on the left side extended ventrally into the tegmentum to the level of the aquaduct. On the left side the optic layers of the colliculus were missing completely. On the right side the posterior and posterolateral margins, totaling approximately one-fifth the surface area, were intact as was the lateral edge of the brachium. In the cortex the knife-cut scars were similar in appearance to those in *Snl* and *Tly* (cf. Fig. 4).

Case Tly. Having obtained only a minor lowering of performance level from the preceding patterns of knife cuts, we decided next to carry the subpial slicing to an extreme. *Tly* was trained to figures A4, B4, C4, D4, E4, and F4 with 290–510 overtraining trials per figure in a total of 153 days spread over a period of ten months. The visual cortex was then sliced bilaterally as shown in Figure 2.

During the first four days after operation *Tly* seemed completely blind. Signs of returning vision were noticed on the fifth day and became rapidly more pronounced during the second week. His postoperative performance is summarized in Table 1. By the 31st day after operation he managed to attain the criterion of 17 correct out of 20 on all his top figures except for the B and E series on which he fell to the third and second levels respectively.

Because his vision seemed to be improving further, *Tly* was retained for later testing after other phases of the experiment had been completed. Meantime in preparation for further studies the training box was remodeled with improvements that raised the normal discrimination levels a little higher than those of the original box. The discriminations which *Tly* was able to achieve on the new box during the following three months are shown in Figure 3A. Judging from the performance of two unoperated cats in the same box, the records of *Tly* would seem to be within, or very close to, the normal range for top capacity in this apparatus.

A new positive triangle and new negative figures A3 and C3 were constructed at one-half the standard dimensions. When tested on these new half-size figures, *Tly* transferred at once with only a few extra errors at the beginning indicating a high degree of equivalence in the two sets of figures. Seventeen correct out of 20 consecutive trials was attained in a total of 22 and 23 trials on the A and C figures respectively. When *Tly* was confronted with two entirely new kinds of patterns at the same reduced dimensions (a square and a circle, each 10.2 mm.^{2} in area, with the circle positive), it

TABLE 1

Postoperative Performance of *Tly*

Days after operation	12			13			15			16	17			19			26		27	28		30				31			32	33	37
Negative figures	B4	B3	B2	C4	C3	C2	F4	F3	F2	D4	E4	E3	E2	A4	A3	A2	B3	B4	B4	C3	C4	F3	F3	F4	F4	A3	A4	A4	B4	E3	D4
Errors	6	8	0	7	5	3	5	5	1	3	4	4	3	4	4	1	8	4	9	2	3	4	1	3	2	2	2	3	13	16	2
Total trials	13	13	20	20	16	20	15	20	20	20	8	9	20	7	16	20	50	15	28	20	20	9	20	10	20	20	3	20	40	43	20

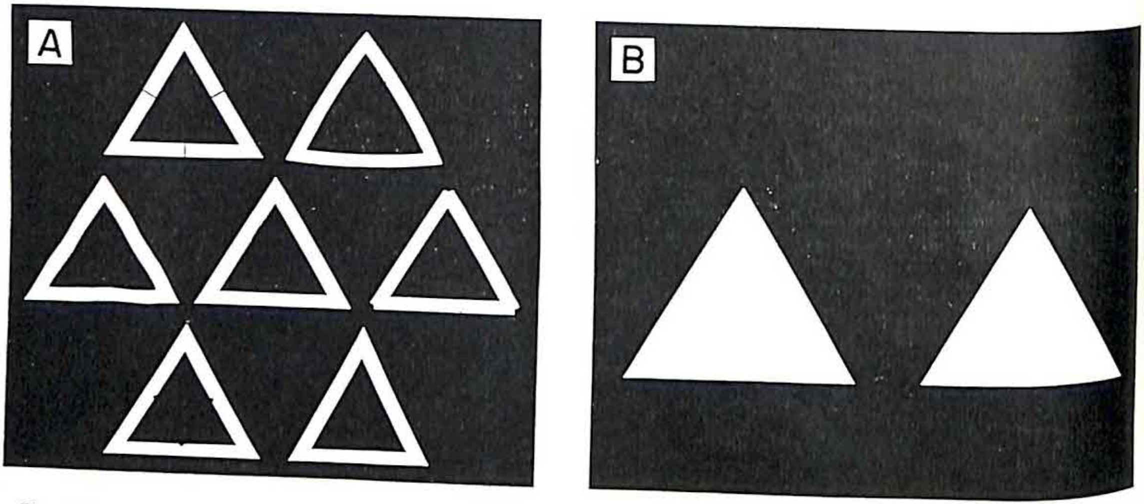

FIG. 3A. Six most difficult negative figures discriminated by *Tly* after operation, with the positive equilateral triangle in center. 3B. Size discrimination learned postoperatively by *Tly*. Sides of the larger triangle measured 7.5 cm. Both A and B are from photostats of the original stimulus cards.

required a total of 357 trials in four days before the learning criterion was achieved.

Capacity for size discrimination was then tested on plain equilateral triangles with the larger triangle positive and with light intensity varied independently of size. In the course of 480 trials in five days, *Tly* achieved criterion on the patterns shown in Figure 3B. Finally, *Tly* learned in 61 trials to discriminate vertical vs. horizontal striations, 1.5 cm. in width.

Histological examination of the cortex showed the visual fields to be effectively partitioned as intended. The majority of the scars extended approximately through the depth of the gray matter (Fig. 4). The cuts tended to be shallow at the edges of the fissures but along the center of the convolutions and on the medial surface of the hemispheres they tended to go a short distance into the white matter. In addition to the small areas of complete cortical destruction indicated in black in Figure 2, additional smaller foci of softening and cavitation were found scattered through the visual areas below the surface particularly where the knife cuts intersected or converged (see Fig. 4). The sliced cortex as a whole had undergone considerable shrinkage which is only partially apparent in the photograph. Diffuse and spotty degeneration was discernible in the lateral geniculate nucleus, pars dorsalis, on both sides.

Wire Inserts

Case Jhn. Following the approach of Lashley, Chow, and Semmes (5), we next tried inserting metallic wires into the cortex to distort the normal pattern of direct current. The first case, *Jhn*, was trained to figures A3, B3, C3, D4, and E3 with approximately 40 overtraining trials per figure in a total of 37 days spread over a period of 3 months. Tantalum wires, gauge 33, were then inserted throughout the visual cortex bilaterally as shown in Figure 5.

When *Jhn* was tested on days 10–16 after operation, a level of 17 correct out of 20, or better, was attained immediately on the B, C, and E figures. After two errors in 16 trials on A3, *Jhn* balked and refused to run further, but ran readily the next day 18 correct out of 20 on A3. A second day and a total of 49 trials were required before 17 out of 20 was attained on D4. Because of motivational complications, it is open to question whether the slight trouble on the A and D figures represented any true deficit of perceptual capacity.

Case Jmm. As in *Snl* (cf. Fig. 2) both superior colliculi plus the left visual cortex were removed prior to training. *Jmm* was then trained to the negative figures A3, B2, C3, D2, and E2 in a total of 56 days spread over four months, including approximately 60 overtraining trials per figure. As with case *Snl*,

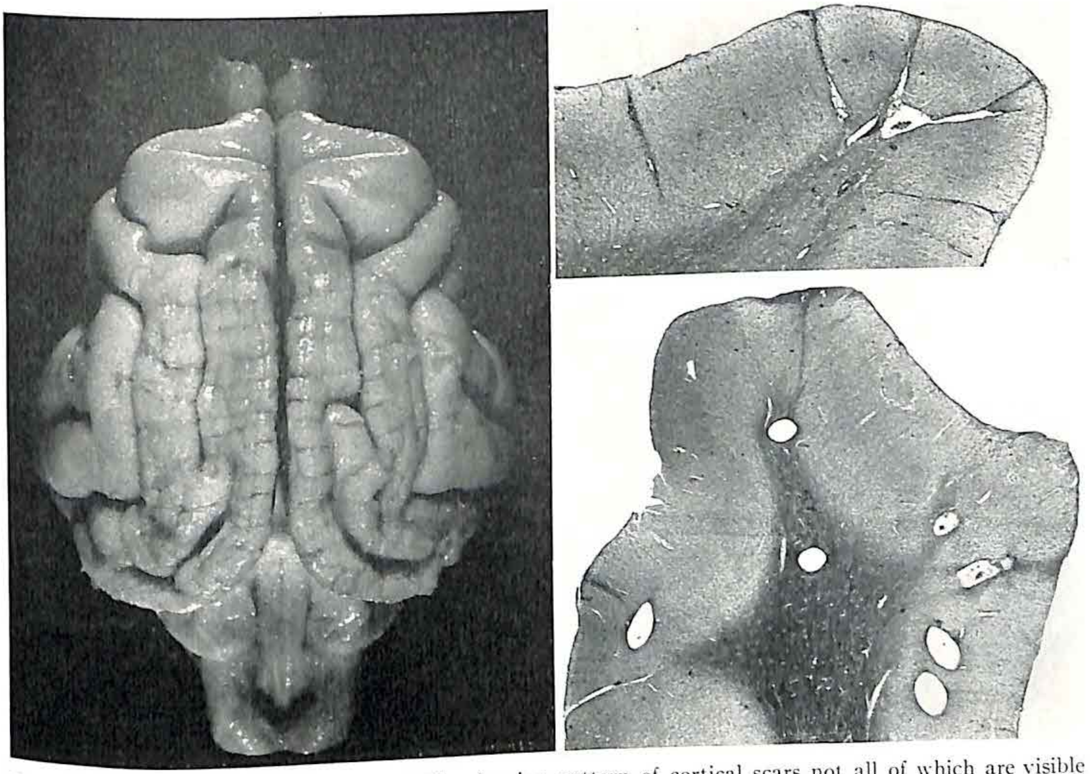

FIG. 4. At left is formalin-fixed brain of *Tly* showing pattern of cortical scars not all of which are visible in the photograph (cf. Fig. 2). At right are photomicrographs of the visual cortex following subpial slicing in *Tly* (top) and after tantalum wire implantation in case *Stf* (below).

learning was below normal in speed and final level of achievement with the cortical and midbrain lesions. Also, the pupils were dilated indicating possible impairment in focusing. The remaining (right) visual cortex was then filled with numerous pins of tantalum wire, gauge 30, much as in *Jhn* shown in Figure 5.

On days 9 to 14 after operation, scores of 18 correct or better were achieved in the first 20 trials on each top test figure. Examination of the brain showed the entire left visual cortex effectively removed and also the optic portion of the left superior colliculus. A thin lateral lip of the superior colliculus remained intact on the right side. The tectal lesions extended on both sides forward into the brachium and pretectal area.

Case Stf. In a total of 61 days spread over a period of four and one-half months *Stf* was trained to figures A3, B4, D4, E3, and F3 including approximately 120 overtraining trials per figure. Tantalum wires, gauge 30, were then inserted throughout the visual cortex of both hemispheres as shown in Figure 5. The postoperative performance is summarized in Table 2. B4 is the only figure on which a criterion score was not achieved on the first attempt. When the negative figures were mixed at random in 94 trials on the last three days, the score was equal to the best of the preoperative records.

Case *Stf* was reoperated upon 44 days after the first operation in an effort to destroy the superior colliculi from a dorsal approach without damaging the visual cortex on either side. As in case *Mrc*, this produced a profound impairment of vision. Recovery was still progressing during the second and third weeks after the operation, and during this period the patterns in columns 1 and 2 of the test scale (see Fig. 1) were the best the cat could discriminate. During the fifth and sixth weeks after the operation, *Stf* again mastered all his top test figures.

On examination of the brain it was found that the anterior two-thirds of the colliculus

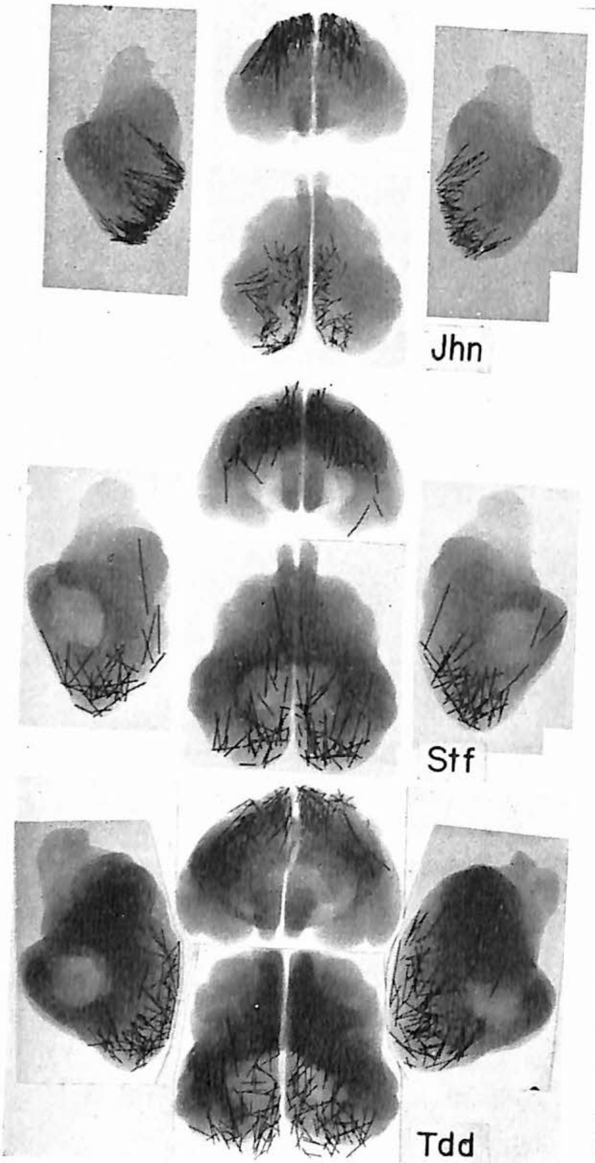

FIG. 5. X-ray pictures of the formalin-fixed cerebral hemispheres of cases *Jhn*, *Stf*, and *Tdd*, taken in three primary planes of the brain to show locations of the implanted wires. Wires tended to migrate in varying degree from their original positions. (Brain of *Jhn* underwent a shrinkage of approximately 17 per cent in linear dimensions as a result of its accidental immersion in alcohol before X rays were taken.)

TABLE 2

Postoperative Performance of *Stf*

Days after operation	10		11		12	13	14	15	16	17	18	19
Negative figures	A3	B4	B4	B3	D4	C4	E3	F3	B4	MS	MS	MS*
Errors	0	4	4	1	1	0	0	1	3	0	0	3
Total trials	20	7	13	20	20	20	20	20	20	30	30	34

* MS—mixed series in which top negative figures were mixed together and presented in random order.

had been removed on the left side including most of the brachium. The collicular lesions went deep into the stratum medullare profundum with some secondary degeneration anteriorly on the left extending ventral to the posterior commissure. On the right side the posterolateral half of the colliculus remained intact including the lateral half of the brachium. The lesion extended forward through the pretectal nucleus and posteromedial portion of the thalamus to the edge of the pulvinar. The functional impairment caused by the second operation in both *Mrc* and *Stf* may well have been correlated more closely with the effects of pretectal and tegmental damage, transection of the splenium of the corpus callosum, pressure on the occipital lobes and interference with circulation in these regions than with the collicular destruction itself.

Case Tdd. Case *Tdd* was trained to figures A4, B4, C4, D4, E4, and F4, including 150–400 overtraining trials per figure in a total of 119 days spread over a period of seven and one-half months. Tantalum wires, gauge 33, were then inserted as shown in Figure 5. The postoperative performance is summarized in Table 3. A4 is the only figure that caused any trouble and this was of questionable significance. *Tdd*'s postoperative record on all the top figures of the test scale is good evidence that dense impregnation of the brain with chemically inert metallic wires does not produce any serious disorganization of pattern perception.

The wires were carefully pulled out of the formalin-fixed brain of *Tdd* and also of *Stf* under a dissecting microscope. In most instances the wires came out cleanly without any adhering layer of tissue. Microscopic examination of the remaining holes (see Fig. 4) showed a wide variation in the degree of scar formation around the wires. In many places there was only a thin film of scar tissue; in others a thick enveloping sheath was present. The thickness of the scar seemed to be correlated with the varying amount of tissue damage caused mechanically by insertion of the wires, being heaviest at points where the damage was

TABLE 3

Postoperative Performance of *Tdd*

Days after operation	14	15	16	17		18	19	20	21	22	23
Negative figures	C4	D4	B4	A4	A3	F4	E4	A4	MS	MS	MS
Errors	0	0	2	3	2	0	2	3	0	1	2
Total trials	20	20	20	8	20	20	20	20	20	20	20

greatest, e.g., where larger blood vessels had been broken.

Cerebellar implants. The entire cerebellum was riddled with implanted tantalum wires in one additional cat otherwise normal. In a second cerebellar case, stainless steel wires were implanted throughout the left half of the cerebellum, while on the right side the wires were inserted and withdrawn in similar locations to equalize the tissue damage on both sides. Functional tests conducted on days 14 through 19 after operation failed to reveal any cerebellar symptoms in either animal.

DISCUSSION

Extensive subpial slicing of the entire visual cortex, or its dense impregnation with metallic wires as described above, failed in either case to produce any marked disturbance of visual pattern perception within the limits of the experimental tests. Good survival of form perception was demonstrated in the ability of the operated animals to discriminate an equilateral triangle from various other triangular figures at a level of performance equal to or closely approaching the preoperative standard.

The absence of a generalized functional breakdown speaks against transcortical intragriseal conduction, including direct current flow, as an important factor in perceptual organization, i.e., in dimensions that might mediate relational effects in form perception.

The stimulus figures were too large to have been projected in most cases into intact cortical tissue between the wires or between the more distantly spaced knife cuts. Furthermore, after operation as well as before, the cats approached the figures more closely—instead of the reverse—when the figures were more difficult. Not uncommonly the operated animals approached the negative figures of all series so closely that the projected retinal patterns must have extended over roughly one-half to two-thirds the entire visual cortex.

The findings in those cases with large bilateral lesions in the tectum discount the possibility that the superior colliculi, or the visual area of the cerebellum to which they relay (9), might have served as substitute centers for the cortical organization. The bordering visual "association" area of the cortex also would seem to be ruled out by the extension of the cuts and the wires into this region.

No abnormalities in visuomotor coordination that could be attributed to the cortical knife cuts or implanted wires were noted at three weeks after operation in casual observations of the cats' ability to jump, to walk a narrow board, or to follow and catch rapidly moving small objects.

It is logically conceivable that, despite perceptual distortions produced by the operations, the positive equilateral triangle may always have appeared less distorted than the negative triangle and been chosen on this basis, or the apparent distortions produced by the operations may have been distinguishable from the actual distortions of the negative figures and were disregarded. These possibilities cannot be rigidly excluded. They are disfavored, however, by the fact that the cats were performing close to the limits of their discriminatory capacity where slight disturbances of any kind tend to cause a breakdown of performance. The distortions caused by the operations ought, theoretically, to have been of such a gross order as to overshadow the lesser actual imperfections that already were reduced to a minimum. Such illusory distortions should frequently have made the positive figure look more distorted than the negative.

The electrical short-circuiting action of metallic conductors inserted in the brain has been discussed at length by Lashley, Chow, and Semmes (5). With or without polarization effects, wires implanted so densely must necessarily have caused considerable distortion in the patterning of any mass "figural" currents. Even in the form of continuously polarized nonconductors, the wires would have destroyed that approximate homogeneity of the cortical tissue that is essential for field theory.

The partial, erratic ensheathing of the wires by scar tissue may have reduced their short-circuiting action. However, if scar tissue has such an effect on current flow, the scars from the subpial knife cuts should themselves have been adequate distorters of field organization.

Since the subpial knife cuts produce a permanent block to ordinary fiber conduction, the results are difficult to reconcile with theories of perception based upon reduplicated interference patterns (4) or upon the alpha rhythm as a scanning device (8). The cuts, involving an erratic invasion of the white matter, should have disrupted any orderly tangential spread of excitations through the gray matter itself or via the short U fibers. The findings seem at present to favor a more vertically organized, motor-conditioned concept of cerebral integration (11).

SUMMARY

To test the importance of transcortical intragriseal conduction in visual pattern perception, the occipital cortex of three cats was subjected to multiple subpial knife cuts intersecting one another in criss-cross patterns and extending through the depth of the gray matter. In four other cases the cortex was densely riddled with tantalum wires inserted in random patterns throughout the visual area and the subjacent white matter. The effects of these operations on perception were tested on a battery of trained form discriminations close to the upper limits of the animals' discriminatory capacity. The general high level of performance after operation indicates that transcortical intragriseal conduction, including direct current flow, is not of critical importance in visual pattern perception.

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DIFFERENTIAL REWARD VALUE OF INCOMPLETE AND COMPLETE SEXUAL BEHAVIOR[1]

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The Miller-Dollard (1, 4) hypothesis concerning the nature of reinforcement in learning assumes that stimulus reduction is a necessary characteristic of a reward. Sheffield, Wulff, and Backer (5) studied the sexual behavior of male rats to discover whether copulatory responses without subsequent ejaculation would serve as a reinforcement for learning. They found that the speed of running of male rats in a straight alley increased when the male was allowed two intromissions and no ejaculation with a receptive female at the end of the alley. Control males, running to other males, did not show as marked a rise in speed of running. Sheffield, Wulff, and Backer concluded that performance of the copulatory pattern without subsequent ejaculation can function as a reinforcement. Since copulation presumably leads to an increase in afferent stimulation, the findings of Sheffield, Wulff, and Backer were not in accord with the Miller-Dollard hypothesis.

The two experiments to be described were attempts to determine whether different degrees of sexual stimulation resulting from goal behaviors would have different amounts of reward value as measured by the learning of a T maze. The three patterns of copulatory behavior affording different patterns of stimulation were (*a*) mounting, thrusting, achievement of intromission, and ejaculation, (*b*) mounting, thrusting, and intromission without ejaculation (hereafter referred to as complete copulation), and (*c*) mounting and thrusting without intromission (incomplete copulation).

EXPERIMENT A

Method

The apparatus used in both experiments is shown in Figure 1 and consisted of a T maze with circular, sheet metal arenas at the end of both arms of the T. The arenas were 20 in. high, and the walls of the maze were 5 in. high. In order to increase the discriminability of the two arms of the maze, the left arm was painted in black and gray stripes and had a wire mesh floor over the wood. The right arm was solid gray and had a plain wooden floor. The start box and stem were painted solid black and had a wooden floor.

The *Ss* were 15 male albino rats from the Sprague-Dawley and Holzmann strains. The stimulus females were brought into estrous by injections of estrogen and progesterone.[3] The 15 sexually mature males, comprising three experimental groups, were housed in individual cages, kept on a 12-hr.-light–12-hr.-dark cycle, and tested during the dark half of the cycle.

The males were trained in the maze under the following conditions: All animals were given four trials each test night. The first and third trials were free, and both choice-point doors were open. The second and fourth trials were forced, the rat being forced to the side opposite the one it had chosen on the preceding trial. When the animal had made its turn at the choice point, the choice-point door was closed to prevent retracing. When the male's hind feet touched the floor of the arena, the arena door was closed, thus preventing re-entering of the arm. Running time was defined as the latency from the raising of the start-box door until the male's hind feet touched the arena floor. The arena on the correct side of the T contained a receptive female; the arena on the incorrect side contained another male rat. The interval between each of the four trials was between 30 and 40 min. The males were randomly assigned either the right or left arm of the T as the correct side.

Group I ($N = 6$) was composed of animals that had experienced one ejaculation prior to the learning trials. When these males went to the correct side, they were given the opportunity to ejaculate with the receptive female. They were allowed 10 min. to display either an incomplete or complete copulatory response and were removed from the arena if no copulatory response occurred. If a copulatory response did occur within 10 min., the male remained with the female until it ejaculated or for a maximum of 10 min. from the first coital response. For all groups, if the experimental rat went

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[3] The hormone used in this study was generously supplied by Dr. Edward Henderson of Schering Corporation, Bloomfield, New Jersey.

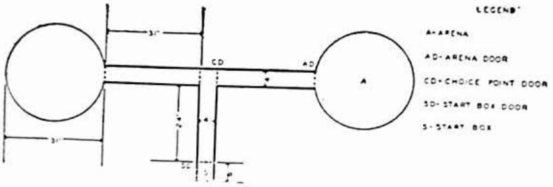

FIG. 1. Schematic diagram of the maze and arenas used in both experiments.

to the incorrect side, it was forced to remain with the second male for 5 min. Males in group I were tested every fourth night for a total of 32 free trials. Group II males ($N = 5$) had experienced several intromissions prior to the training but had never ejaculated. These males were run under the same conditions as group I except that they were allowed only two intromissions each time they were with the receptive female and were never permitted to ejaculate. They were tested every fourth night for a total of 32 free trials. Group III males ($N = 4$) had experienced intromission prior to the training, but, like group II males, no ejaculation occurred before or during the experiment. These males were treated exactly like the group II males except that their schedule consisted of tests two nights in succession, then two nights of no testing, then two nights of testing, etc. This group received a total of 64 free trials.

Results

Errors in the maze. Figure 2 shows the percentage of the free trials in which the males went to the correct side, i.e., the one containing the receptive female. Group I males showed an initial increase in correct runs which leveled off at 100 per cent at the end of training. Group II males showed no significant change in correct runs over the course of training. For the last four trials (29 to 32), group I made significantly more correct runs than group II ($p < .01$). (All stated p values are for one tail.) Group III males showed an initial increase in correct runs; the mean of trials 1 to 4 was lower than the mean for trials 9 to 12 ($p < .05$). However, this increase was followed by an equally significant decrease in correct runs.

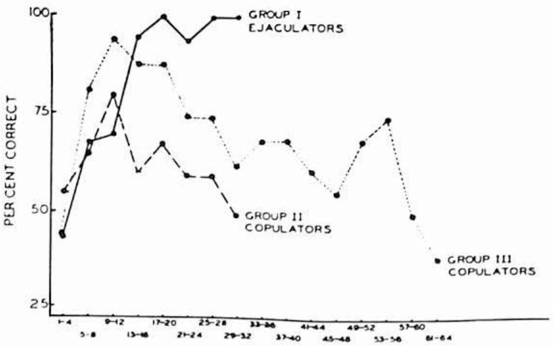

FIG. 2. Percentage of the free trials in which the male went to the side containing the receptive female.

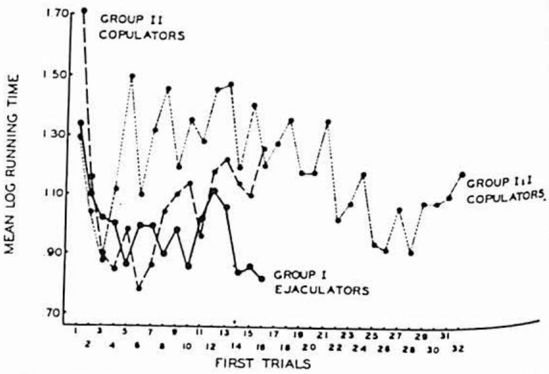

FIG. 3. Mean log of the running time through the maze for the first trial of each test night.

Running time in maze. Figure 3 demonstrates the mean log of the running time for the first free trial of each test night. Although all three groups showed a sharp initial drop in running time, groups II and III displayed a marked rise in running time following this initial decrease. Comparing the means for the final four trials (13 to 16) reveals that group I males were running faster than group II ($p < .01$).

Frequency of complete and incomplete copulatory responses with the receptive female. Figure 4 deals only with those trials, free and forced, in which the male went to the receptive female. It shows the percentage of such trials in which one or more complete or incomplete copulatory responses occurred. These will be referred to as copulatory positive trials. Group I males, allowed to ejaculate, responded in every one of the 32 trials. Group II males, allowed only intromissions, showed a marked decrease in copulatory positive trials; the difference between trials 1 to 8 and 25 to 32 was significant at the .05 level of confidence. Group III males, also prevented from ejaculating, showed a significant decrease in copulatory positive trials when trials 1 to 16 are compared with trials 49 to 64 ($p < .05$).

A comparison of the maze performance of group I with that of groups II and III indicates that intromission without ejaculation

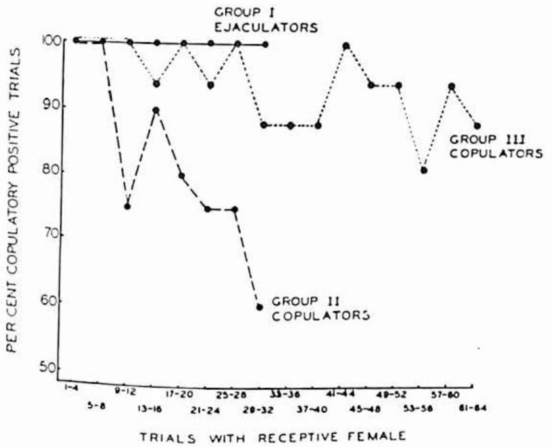

FIG. 4. Percentage of the trials with the receptive female in which the male engaged in copulatory behavior.

was not as effective a reward as intromission with ejaculation. In addition, the decreased tendency to engage in copulatory behavior displayed by groups II and III suggests that the occurrence of intromission without ejaculation may eventually weaken the tendency to initiate coital reactions. A second experiment was planned in order to check these results. In Experiment A the N's were small and the groups had different sex histories prior to the training. In addition, the data from Experiment A offered no clue as to which aspect of the copulatory pattern was leading to the inhibition of coital behavior in groups II and III. This inhibition could be the result of repeated experiences of intromission without ejaculation or the result of mounting and thrusting alone with actual penetration of the vagina having no effect on the development of the tendency to inhibit sexual behavior. The second experiment was an attempt to provide a partial answer to this question.

EXPERIMENT B

Method

The *S*s were 46 sexually mature male albino rats of the Holzmann strain. The three groups of males used in Experiment B were maintained like those in Experiment A and trained in the same maze. The procedure was identical to that of Experiment A with the following exceptions: The correct side of the maze contained a receptive female; the incorrect side contained a spayed, nonreceptive female whose vagina had been closed surgically and, therefore, could not be penetrated by a male. All animals were run two free trials every third night for a total of 54 free trials. Trials were between 40 and 60 min. apart, and no forced trials occurred. No male had experienced intromission or ejaculation prior to the learning trials.

For a correct run, group E males ($N = 14$) were given an opportunity to ejaculate with the receptive female. Group C males ($N = 16$) were allowed to achieve two intromissions with the receptive female but were not allowed to ejaculate. Group T males ($N = 16$) were given an opportunity to mount and thrust a receptive female whose vagina had been closed surgically, thus preventing intromission. Animals in all groups were allowed 10 min. in which to make a copulatory response. For groups E and C the time limits were identical to those of groups I and II in Experiment A. For group T, if a coital response occurred within this 10-min. time limit, the male remained with the female for 5 min. following the first incomplete copulatory response. For all groups, if a male went to the incorrect side, he remained with the nonreceptive, surgically closed female for 5 min.

Results

Since only free trials were used in Experiment B, there was no way of guaranteeing that a male would be with the receptive female each test night. Being with the nonreceptive female, on the incorrect side, may have functioned as a social reward, and many animals that began training by going to the incorrect side continued to do so for many trials. Therefore, there were a great many animals that chose the correct side only a few times over the course of training, and, hence, had very few copulatory positive trials. These animals behaved differently from those males that had many copulatory positive trials, and it was decided to analyze separately the data of the 8 animals from each group that showed the greatest number of copulatory positive trials. The data for these 24 sexually active males will be reported here. The data for the 22 animals showing the least number of copulatory positive trials were analyzed and appear in the original dissertation (2).

Maze errors. Figure 5 shows the mean percentage of first trials of each test night in which the male went to the correct side. For all three groups, there is a significant increase in correct runs for trials 4 to 6 as compared with trials 1 to 3 ($p < .05$). At the end of training, all three groups made more correct runs than initially, and comparisons between trials 1 to 3 and trials 25 to 27 for groups E,

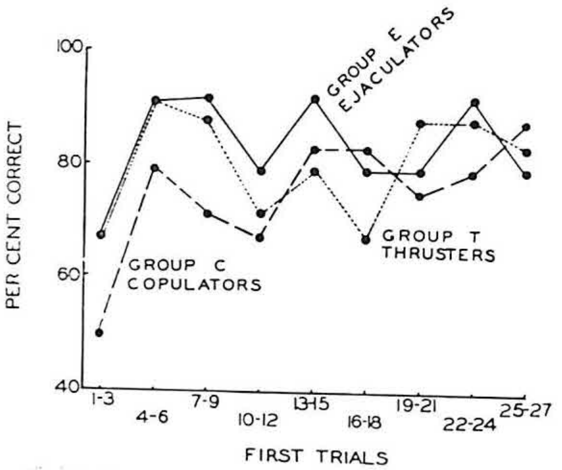

FIG. 5. Percentage of first trials in which the male went to the side containing the receptive female.

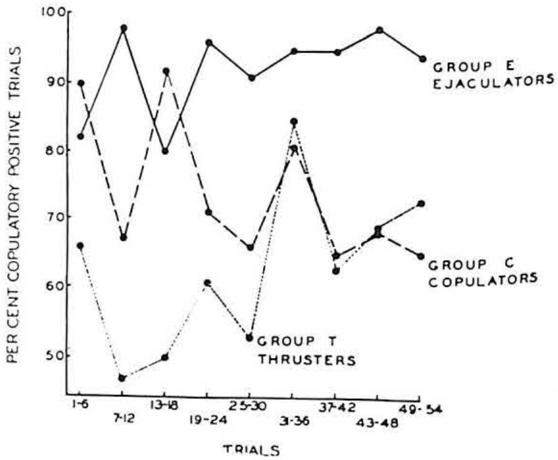

FIG. 7. Percentage of the trials with the receptive female in which the male engaged in copulatory behavior.

C, and T yield p values of .07, .03, and .07, respectively.

Running time in the maze. Figure 6 illustrates the mean log of the running time through the maze for the first trial of each test night. There was a significant drop in running time for all groups during the first half of training. However, the leveling off in running times was uneven, and for trials 13 to 27 the running times of group C males were significantly lower than those of group E ($p < .05$) and group T ($p = .07$).

Frequency of copulatory responses on trials with the receptive female. Figure 7 shows the percentage of the trials with the receptive female in which one or more incomplete or complete copulatory responses occurred. Group E males showed a gradual increase in the number of copulatory positive trials. Group C males showed a steady decrease in the tendency to engage in copulatory behavior, and the difference between trials 1 to 6 and 49 to 54 is significant at the .06 level of confidence. Group T males showed no significant change in the percentage of copulatory positive trials over the course of training; however, group T males showed a steady decrease in the mean number of incomplete copulatory responses effected on each trial in which at least one incomplete copulation occurred. For the first 18 trials Group T males made an average of 9.8 incomplete copulatory responses per test; for trials 19 to 36, a mean of 8.4 copulatory attempts; and for trials 37 to 54, a mean of 6.6 coital responses. The difference between trials 1 to 18 and 37 to 54 is significant ($p < .02$).

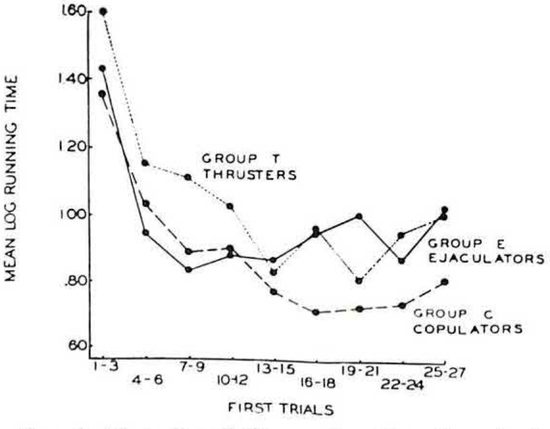

FIG. 6. Mean log of the running time through the maze for the first trial of each test night.

DISCUSSION

In both experiments the males that were allowed to ejaculate, groups I and E, showed an increase in correct runs, in speed of running, and in the tendency to engage in copulatory behavior over the course of training. This suggests that ejaculation functioned as a reward for both the instrumental behavior of maze learning and the consummatory response of copulation. However, the males that were not allowed to ejaculate with the receptive female, groups II, III, C, and T, showed the puzzling combination of a decreased tendency to effect the goal response and an increased tendency to make correct turns in the maze. The males in the four groups not allowed to ejaculate showed a significant decrease in the tendency to engage in coital behavior as training progressed, but with respect to correct runs, group III showed an initial increase and groups C and T showed an over-all increase. The decrease in the tendency to engage in coital behavior displayed by these males suggests that incomplete or complete copulation without ejaculation results in a gradual inhibition of the innate tendency to engage in coital behavior. However, the increase in correct runs indicates that some aspect of the complex pattern of copulation without ejaculation can function as a reinforcement according to classical operational definitions of reward. It seems that different aspects of the copulatory pattern have both a punishing and rewarding effect, for the total pattern leads to a decreased predisposition to copulate and some increase in the tendency to go to the receptive female.

Because of the lack of relevant data, there is no empirical basis for hypothesizing which aspect of the copulatory pattern is rewarding and which punishing. It is possible that stimulation of the glans penis is temporarily rewarding, but repeated experiences of penile stimulation without subsequent ejaculation are punishing in nature. An alternative hypothesis is that any stimulation of the penis which is not followed by ejaculation is punishing, and the rewarding stimuli include olfactory, visual, or other tactile stimulus patterns.

In any event, the fact that copulation without ejaculation is both rewarding and punishing suggests that, with training, the males in groups II, III, C, and T would be in an approach-avoidance conflict. It is assumed that each experience of copulation without ejaculation strengthens a habit which leads to an inhibition of further coital responses, and this inhibition or avoidance habit soon competes with the innate tendency to initiate copulatory behavior. It is further assumed that with each copulatory attempt the strength of the avoidance habit is increased much more than that of the approach tendency. Theoretically, after a sufficient number of coital experiences with the female, the avoidance habit should become as strong as the approach tendency, and at this point the male will begin to inhibit copulatory behavior.

According to Miller's analysis of approach-avoidance behavior (3), the tendencies to approach or avoid a goal (in this case the goal is the receptive female) are stronger the nearer the animal is to the goal. However, the strength of the avoidance tendency is assumed to increase more rapidly with nearness to the goal than the strength of the approach tendency. That is, the avoidance habit generalizes more steeply than the approach tendency, and, therefore, although the avoidance response may be stronger than the approach tendency in the arena, it may be weaker than the approach tendency at the choice point of the T maze.

In Experiment A the males not allowed to ejaculate, groups II and III, showed both a decreased tendency to copulate and a decrease in correct runs and in speed of running. This indicates that the avoidance tendency had generalized back to the stimuli of the maze and was competing with the approach tendency in both the arena and in the maze proper. In Experiment B, groups C and T showed the decreased copulatory tendency but did not show the decrease in correct runs or in speed of running. In fact, group C males were running faster than group E males during the latter half of training. This suggests that the avoidance habit had not yet generalized back from the stimuli of the arena to the stimuli of the maze.

The present data and theoretical analysis suggest that in Experiment A the avoidance tendency became strong early in training for the males that were not allowed to ejaculate. The results from Experiment B indicate that the avoidance response did not become strong until quite late in training. This difference could be due to the fact that the forced-trial procedure guaranteed the occurrence of copulation experiences at the beginning of training; this was not so in Experiment B. This early competition between the approach and avoidance tendencies in Experiment A may have greatly facilitated the rapid development of a strong avoidance habit.

These results are not in complete accord with either the stimulus reduction position of

Miller and Dollard or the contiguity position of Sheffield, Wulff, and Backer. The hypothesis that stimulus reduction characterizes reinforcement would not have predicted the significant increase in correct runs shown by some of the males not allowed to ejaculate. On the other hand, Sheffield, Wulff, and Backer suggest that the elicitation of a prepotent consummatory response, like copulation, is the critical factor in the reinforcement of instrumental reactions. The significant decrease in the tendency to copulate shown by the males not allowed to ejaculate is not in agreement with this hypothesis. The data suggest that a more complete analysis of the complex stimulus patterns involved in rodent mating behavior is needed before any definitive statements can be made concerning the relevant mechanisms of reinforcement.

SUMMARY

Male albino rats were trained in a T maze in order to determine possible differences in the reward value of three patterns of sexual responding.

In Experiment A, three groups of males were run two free and two forced trials each test night. The correct side of the T contained a receptive female, the incorrect side contained another male. Group I males were allowed to ejaculate with the receptive female. Rats in groups II and III were allowed only two intromissions with the receptive female and never ejaculated. The results showed that group I was superior to groups II and III in terms of errors in the maze and in the tendency to effect copulatory responses. Groups II and III showed a significant decrease in the tendency to engage in coital behavior as training progressed.

In Experiment B, three groups of males were run two free trials a night. Group E males were allowed to ejaculate while mating with a receptive female; group C animals were allowed only two intromissions; and rats in group T were allowed only to mount and thrust a receptive female whose vagina had been surgically closed. For all groups the incorrect side of the T contained a nonreceptive female with a surgically closed vagina. With training, group E males showed increased sexual responsivity with the female and decreasing errors in the maze. Groups C and T showed a decreased coital responsivity with the female, but an increase in correct runs over the course of training.

It was concluded that although sexual responding short of ejaculation motivates the acquisition of a habit which inhibits further copulatory behavior, certain aspects of the mating pattern can function as rewards for instrumental learning.

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CLASSICAL CONDITIONING IN THE PLANARIAN, *DUGESIA DOROTOCEPHALA*

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The investigation of learning in animals phylogenetically below the earthworm has been focused chiefly on the protozoans (3). Such animal groups as sponges, jellyfish, and ctenophores have been largely neglected. The flatworm group has received some attention from Hovey (1), who reports primitive behavioral modifications of the type known as "negative adaptation"—the extinction of innate sensory-motor reflexes. Hovey partially extinguished in leptoplanid polyclads the locomotor response initiated by the onset of photic stimulation. As soon as *S* started to move following exposure to the light, Hovey stopped its motion temporarily by touching the animal on its anterior region. Although no worm could be trained to remain motionless to photic stimulation lasting 5 min., the number of touches occurring on a single trial decreased markedly with progressive training. Similar work on negative adaptation in flatworms has been carried out by Soest and Dilk (reported in 2).

From the standpoint of evolution the planarian, the commonest free-living flatworm, is an especially significant animal. Such evolutionary advancements as true synaptic nervous transmission, definite encephalization, and bilateral symmetry, to mention only a few, appear for the first time in planaria. On the basis of these developments in the planaria, one would think it possible to establish behavioral modifications in them of greater complexity than that of negative adaptation. Dilk seemingly obtained classical conditioning in these organisms, but proper control groups were omitted in his study. No other studies report classical conditioning in flatworms.

The purpose of the present experiment was to determine the facility with which planaria develop conditioned responses (CR's) under conditions of massed training. The unconditioned stimulus (US) was a weak electric shock which consistently evoked a longitudinal contraction of the animal's entire body. A change in illumination served as the conditioned stimulus (CS).

METHOD

Subjects

Forty planaria (*D. dorotocephala*), varying in length from 14 to 22 mm., were studied. They were obtained locally and placed in a glass aquarium, the dimensions of which were 12 in. by 7 in. by 5.5 in. The water depth was maintained at about 3 cm., and the water was changed regularly. The aquarium was placed in a room whose temperature ranged between 22° and 24°C. Artificial and natural lighting was kept at a minimum. Snail meat was occasionally provided as food.

Apparatus

The main part of the apparatus consisted of a plastic trough, semicircular in shape, 30 cm. in length, 3 cm. wide, and 1.5 cm. deep. The trough was attached at both ends to plastic supports which were in turn mounted firmly on a 1-in.-thick plywood base. The trough was filled with aquarium water to a depth of 12 mm. At either end of the trough were mounted soldered electrodes. A direct current of 28 ma. passed through the water was used as the US. The entire apparatus was set on a table relatively free from vibration. A goose-neck lamp housing two 100-w. lights was centered 1 ft. directly above the trough and constituted the source of the CS. Overhead at a height of 12 ft. was a 40-w. light providing general illumination. The apparatus was slightly displaced to one side of the overhead light to eliminate the casting of shadows on the trough.

Procedure

Only one *S* was studied at a time. The *S* was transported from the aquarium to the trough in a pipette. The *S* was allowed to "explore" the trough for 10 min. before experimental training was begun. After an initial period of disturbance during which the animal's locomotion was ditaxic or ameboid, it generally began to move in a normal fashion on the bottom of the trough. This movement may be described as "gliding," accomplished by ciliary activity. When *S* reached the end of the trough, it would turn and retrace the trough. Occasionally *S* would come to rest and would remain motionless. If this "sleep" state continued for more than 1 min., *S* was prompted to locomotion by water currents set up by a pipette. Trials were given only when *S* was gliding in a straight line and was oriented toward either of the electrodes.

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The *S*s were divided roughly in terms of length into four groups of 10 *S*s each: the experimental group (group E), the light control group (group LC), the shock control group (group SC), and the response control group (group RC).

Group E was given a total of 150 trials, each trial consisting of a light-shock pairing. The duration of the light was 3 sec.; that of the shock was 1 sec. The US overlapped the light on the last second of its presentation. All responses occurring during the initial 2-sec. period of the light were recorded. Training was carried out in three blocks of 50 trials each. A 5-min. interval separated each block. The intertrial interval was approximately 20 sec.

For group LC, 150 trials were administered in the same manner as for group E, except that the US (shock) was never given. The light lasted for 3 sec., and responses were recorded only if they appeared during the first 2 sec.

To determine if the shock sensitized the animal to the light stimulus, group SC was given a total of 150 shock trials, each trial lasting for 1 sec. After every five shock trials, 1 test trial was given which consisted of the presentation of the light alone for 3 sec. In this case, three blocks of 60 trials were presented, 50 shock trials and 10 test trials in each block. Thus a total of 30 test trials was obtained. All responses occurring during the first 2 sec. of the light were recorded.

Group RC was employed to determine the number of "spontaneous" responses which one might expect to occur without stimulation from either shock or light. For this group, 150 trials of 3-sec. duration were given during which no experimental stimulation of any kind was administered to the animals. All responses that occurred during the initial 2 sec. of each trial were recorded.

RESULTS

Two distinct responses were observed in *S*s during the test periods. These two responses were: (*a*) a sharp turning of the cephalic region to one side or the other, and (*b*) a longitudinal contraction of the entire body. In general, only one of the two types of responses appeared on a single trial.

Figure 1 presents the percentages of turns, contractions, and a combination of these two responses which occurred during the course of training for groups E, LC, and RC. It will be seen that the turning response was predominant for all three groups. For group E the frequency of turns as well as the frequency of contractions increased as a function of training. The combined curve for this group suggests that further massed training would have resulted in a performance asymptotic at some point just below the 50 per cent level of response frequency. For groups LC and RC the combined curves indicate some decrement

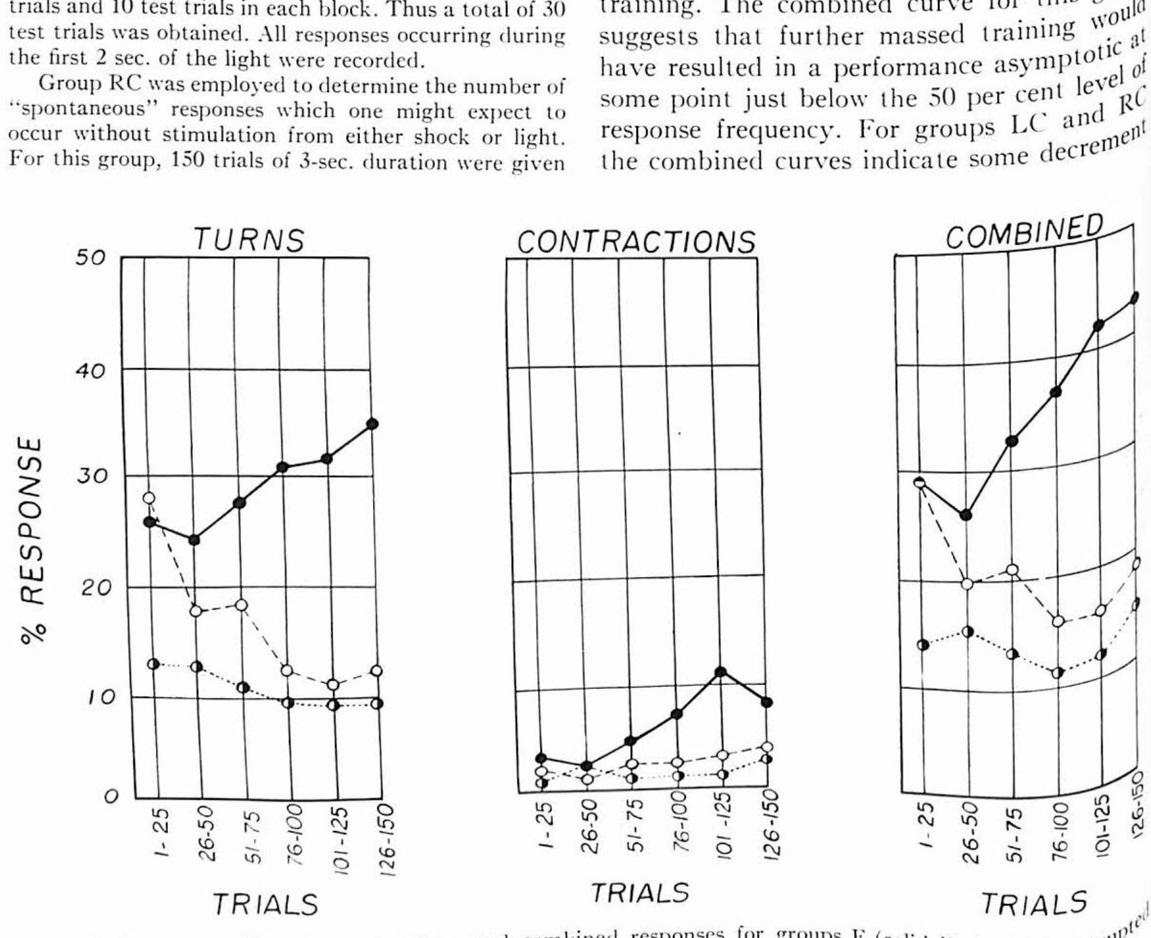

FIG. 1. Percentage of turns, contractions, and combined responses for groups E (solid line), LC (interrupted line), and RC (dotted line).

TABLE 1

Mean Turns, Contractions, and Combined Responses on the First 50 and Last 50 Trials for Groups E, LC, and RC

Group	Response	First 50 Trials	Last 50 Trials	Diff.	p
E	Turns	12.6	16.6	4.0	.01
	Contractions	1.2	5.0	3.8	.01
	Combined	13.8	21.6	7.8	.01
LC	Turns	11.7	7.6	−4.1	.01
	Contractions	0.6	2.1	1.5	
	Combined	12.3	9.7	−2.6	
RC	Turns	10.1	7.7	−2.4	.05
	Contractions	0.7	0.9	0.2	
	Combined	10.8	8.6	−2.2	

TABLE 2

Percentage of Combined Responses for Group E

Length (mm.)	Animal No.	Trials					
		1–25	26–50	51–75	76–100	101–125	126–150
14	1	16	8	40	16	52	44
15	2	16	12	16	16	40	36
14	3	24	16	36	40	32	52
20	4	24	16	24	28	36	52
18	5	36	28	28	48	28	44
15	6	20	48	44	44	76	44
22	7	44	48	52	64	60	68
15	8	40	40	36	40	40	32
14	9	44	24	28	48	28	28
20	10	24	24	24	32	36	36

TABLE 3

Mean Turns, Contractions, and Combined Responses on the First 15 and Last 15 Test Trials for Group SC

Response	First 15 Test Trials	Last 15 Test Trials	Diff.*
Turns	5.4	4.2	−1.2
Contractions	0.2	0.4	0.2
Combined	5.6	4.6	−1.0

* None of the differences is significant at the .05 level of confidence.

in the frequency of responses as a function of trials.

In order to determine the significance of the increment or decrement in response frequency for each of these three groups, the data for the first 50 trials were compared with those for the last 50 trials. Table 1 summarizes this information. Wilcoxon's nonparametric test for paired replicates (4) was employed because of the lack of homogeneity of variance as well as the nonnormality of the distributions. The data for group E exhibit a very significant increment in the frequency of turns and contractions, as well as of the combination of these responses. For groups LC and RC there was a significant decrement in the frequency of the turning response, while the frequency curves of the contractions and of the total responses (turns and contractions combined) remained essentially unchanged throughout training.

In terms of the total number of responses during the 150 trials, group E made significantly more turns and significantly more contractions than either group LC or group RC. Wilcoxon's test for unpaired replicates (4) revealed p values at the .01 level for turns and at the .02 level for contractions. The differences between group LC and group RC were not significant.

Table 2 gives the individual data for group E in terms of percentage of combined responses for each block of 25 trials. It can be seen that of the ten *S*s in this group, only three failed to show any evidence of conditioning (animals 5, 8, and 9). The length of *S* appears to play no important role in the facility of conditioning planaria.

The data obtained from group SC (shock control group) appear in Table 3. In order to determine if repeated shock trials sensitized *S*s to the light stimulus, the responses on the first 15 test trials were compared with those on the last 15 test trials. The differences do not approach any respectable level of significance in terms of the frequencies of turns, contractions, or of total responses.

DISCUSSION

Figure 1 clearly shows that CR's can be established in planaria. For group E the frequency of turns as well as the frequency of contractions increased significantly with training. That these results are not attributable to increased sensitivity to the photic stimulus is shown by the performance of the light control group (group LC). Further evidence that repeated presentation of the light failed to produce a condition of "sensitization" is shown by the lack of any significant difference between the response frequencies of groups LC and RC. From this result, it would seem that the light was a neutral stimulus and that the responses which did occur in groups LC, SC, and RC were spontaneous. The initial level of response frequency in group E was also apparently the result of spontaneous reactions. The shock control group (group SC) provides data which clearly indicate that pseudo-conditioning was an improbable factor in the performance of group E, since repeated shock stimulation did not cause a significant increment in response frequency to the light. The results obtained from group SC likewise eliminate the possibility that any increased generalized activity level was the cause of the increment in response frequency exhibited by group E.

Of particular interest was the significant increment in the number of turning responses made by group E with progressive training. The US invariably evoked a longitudinal contraction of the entire body, but seldom was accompanied by a turning of the anterior region—the latter occurring less than 5 per cent of the time. In group E, however, not only was there an increment in the number of contractions, but there was, as well, a similar increment in the number of turning responses. This discrepancy between the nature of the UR and that of the CR would seem to suggest a form of "expectation" learning or avoidance learning in the planarian. A more parsimonious explanation, however, is available for this discrepancy. The turning response may have been a part of the unconditioned reaction, but was obscured by the more generalized contraction of the entire body.

Comparisons of habit formation in the planarian with those of neighboring animal groups cannot be made at the present time because of insufficient data. But one might expect that the acquisition of simple associations will not serve to help us differentiate among animals on the basis of "intelligence."

SUMMARY

The purpose of the present experiment was to study the facility with which planaria (*D. dorotocephala*) form CR's in a classical light-shock conditioning situation. Forty animals were employed. They were divided into four equal groups: the experimental group and three different control groups.

It was found that for the experimental group there was a significant rise in the number of contractions and turning responses as a function of the number of trials. That these increments in frequency of responses were not caused by sensitization to either shock or light stimulation was indicated by the performance of the control groups.

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REACTIONS OF THE MEALWORM, HONEYBEE, AND COCKROACH TO SOME CARBON DIOXIDE CONCENTRATIONS

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The psychological and biological literature contains frequent reference to approach or avoidance behavior in the lower organisms. Implicit in much of this work is the following logic: (*a*) Certain environmental conditions are optimal for the organism; (*b*) nonoptimal or "dissatisfying" conditions will instigate behavior eventuating in (*c*) locomotion to a region of optimal ("satisfying") conditions where (*d*) the locomotory behavior decreases.

Shelford (6) has presented convincing evidence that the preferred stimuli, as demonstrated in approach-avoidance behavior, are related to the normal habitat of the animal. More recently, Fry (2) has extended this thinking, taking into consideration such factors as acclimation and the presence of additional stimuli that tend to amplify, attenuate, or otherwise alter the response to the stimulus in question. Both of these investigators exposed their animals to stimulus gradients, recording the stimulus intensity or concentration at the point where the animals congregated. Neither Shelford nor Fry was concerned with response thresholds.

It is the thesis of the present paper that the *range* of stimulus intensities to which an organism responds in an approach-avoidance situation is a function of the normal habitat of the animal. More specifically, using organisms with roughly similar respiratory systems, we expected that the range of carbon dioxide concentrations evoking avoidant behavior would be a function of the organism's potential exposure to carbon dioxide in the normal habitat.

METHOD

Subjects

The *Ss*, randomly selected from the laboratory colonies, were 25 mealworms (*Tenebrio molitar*), 30 honeybees (*Apis mellifica*), and 40 cockroach nymphs (*Periplaneta americana*).

Apparatus

The apparatus, suggested by Jones (4), was a 32-cm. by 2.5-cm.-diameter Lucite tube with gas inlets at both ends, a screened outlet at the bottom center of the tube, and a stoppered opening in the center top for inserting the animal (Fig. 1). The top opening was cut to receive the ground neck of a 20-ml. weighing bottle. The device effectively produced two contrasting and sharply differentiated supplies of gas into and out of which the animal could freely move.

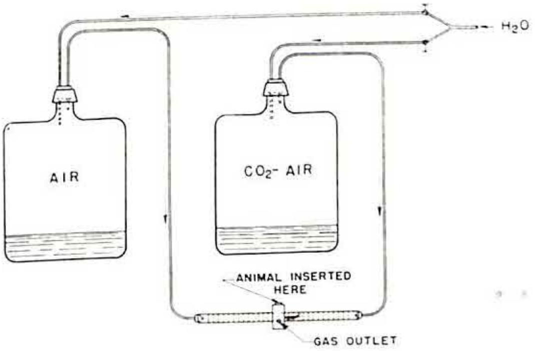

FIG. 1. Gas supply and discrimination tube.

The diffusion and mixing of gases at the choice point was tested by admitting nitric oxide into one end of the discrimination tube, and air into the other, at the rate of 50 ml. per minute. The two colorless gases react to form the familiar brownish nitrogen dioxide, permitting visual evidence of diffusion of either gas into the other end of the tube. There was little evidence of diffusion more than 1 cm. from the center of the tube, and no diffusion beyond 2 cm.

The gas supply used in the experiment was from two 10-gal. bottles, one containing air and the other carbon dioxide or a carbon dioxide–air mixture. Four percentage concentrations of carbon dioxide were used: 100, 50, 25, and 10. The gases, displaced by a 50 ml. per minute flow of water into the bottles, were led to either end of the discrimination tube.

Since carbon dioxide is highly soluble in water, supplying the gas by displacement with water should produce some variation in the carbon dioxide concentration from trial to trial. To check this possibility gas samples taken at the beginning and end of the trials were analyzed. The percentage concentrations were as follows: 99.4 to 96.3, 51.0 to 39.2, 26.8 to 21.1, 13.6 to 7.9.

Procedure

Individual *Ss*, randomly assigned to the experimental groups as indicated in Table 1, were kept in 20-ml. weighing bottles during the experiment.

With the carbon dioxide–air mixture entering one end of the tube and atmospheric air the other end, a weighing bottle was inverted over the center opening, and an animal permitted to drop to the choice point. The bottle was then removed, a stopper inserted in the opening, and the animal's entries into either alley ob served for a 5-min. period or until anesthesia occurred. The criterion of alley entry, selected on the basis of the gas diffusion data, was a 2-cm. penetration into either alley. At the end of 5 min. the weighing bottle was again inserted in the top opening, the animal shaken into the bottle, and the tube cleaned by a blast of high-pressure air. The gas supply was then reversed, left for right, the animal again inserted into the tube, and observed for a second 5-min. period. Half the animals were tested with the air first to the right side, and half with the air first to the left. In all cases, if an animal stayed in either end of the tube for 2 min., it was removed to the weighing bottle and restarted.

If anesthesia occurred, the timer was stopped and the insect removed to a weighing bottle. Upon recovery the animal was returned to the apparatus and the trial resumed. Criteria of recovery were pretest respiration and resumption of apparently normal activity.

RESULTS

The results are summarized in Table 1. The second row for each concentration indicates the proportion of entries into the air end of the tube. Mealworms demonstrated a clear preference, choosing air over carbon dioxide at the 100 per cent concentration, the threshold for this behavior being somewhere between the 50 per cent and 100 per cent concentration.

Honeybees showed a clear preference for air over the carbon dioxide mixtures at the 50 per cent and 25 per cent concentrations, but were apparently unable to discriminate between air and 100 per cent carbon dioxide, the latter producing anesthesia on each carbon dioxide entry. Three bees were anesthetized when their response at the choice point was delayed.

Cockroaches avoided the carbon dioxide mixture only at the 10 per cent concentration. Evidence that the 25 per cent concentration is near the upper preference threshold for cockroaches is afforded by the fact that four of the insects showed a consistent preference for air over this concentration of carbon dioxide. With the exception of one cockroach, the one anesthetized, the first carbon dioxide entry was followed by hyperactivity. The insects rapidly moved from one end of the tube to the other, resulting in a high frequency of response and chance performance.

The incidence of anesthesia among the bees at the 50 per cent and 25 per cent concentrations was five, and three, respectively. In the first case two bees, and in the latter one bee accounted for these frequencies. In each case the failure to demonstrate a preference followed several "air" responses, during which the bees were necessarily exposed to carbon dioxide. This exposure produced a general retardation of behavior and more rapid anesthesia on subsequent carbon dioxide entry.

The cockroaches at the 50 per cent and 100 per cent concentrations and the bees at the 100 per cent concentration all showed more entries to the carbon dioxide side than to the air side. This asymmetry is not suggestive of a preference for carbon dioxide, but is merely an artifact of the test situation. Entry into the air side may be followed by carbon dioxide entry, but carbon dioxide entry is followed by anesthesia.

The third row for each carbon dioxide concentration in Table 1 indicates that the incidence of anesthesia for cockroaches at the 50 per cent and 100 per cent concentrations and for bees at the 100 per cent concentration is

TABLE 1

Responses, Air Entries, and Anesthesia

Variable	Mealworm	Honeybee	Cockroach
100 Per Cent CO_2 Concentration			
N	10	10	10
Number of responses	48	31	27
Proportion air entries	.77*	.35	.48
Incidence of anesthesia	3	23	14
50 Per Cent CO_2 Concentration			
N	10	10	10
Number of responses	52	62	40
Proportion air entries	.50	.76*	.40
Incidence of anesthesia	0	5	16
25 Per Cent CO_2 Concentration			
N	5	10	10
Number of responses	24	63	86
Proportion air entries	.54	.86*	.58
Incidence of anesthesia	0	3	1
10 Per Cent CO_2 Concentration			
N			10
Number of responses			103
Proportion air entries			.73*
Incidence of anesthesia			0

* $p < .01$.

directly related to the failure of the discrimination mechanism. This was not true, however, of mealworms at the 50 per cent and 25 per cent carbon dioxide concentrations, where the gas apparently had no deleterious effect within the 5-min. observation periods.

DISCUSSION

These data may be related to the normal habitat of the species tested. The cockroach dwells generally in an environment of atmospheric air; carbon dioxide rarely increases to any great extent. Under conditions where some increase occurs, opening of the spiracles, increased limb and alar movements, and the accompanying increased ventilation are generally adequate compensation for a nonadequate environment. Slightly higher concentrations produce avoidant behavior.

Our data suggest that at the 50 per cent and 100 per cent carbon dioxide concentrations, where the above mechanisms are not adequate, the cockroach has no subsidiary adjustment potential. It neither avoids the carbon dioxide nor approaches the air consistently. The likelihood of survival is very low.

The honeybee, while generally exposed to atmospheric air in its normal environment, may at times engage in behavior that markedly increases its exposure to carbon dioxide. In its "cluster" behavior, by which intra-hive temperature is controlled, close physical proximity to other bees with the ensuing reduction in circulation of atmospheric air results in increased carbon dioxide concentrations within the cluster. The bees in the present experiment demonstrated an ability to discriminate air and 25 per cent or 50 per cent carbon dioxide, avoiding the latter. This ability was not apparent at the 100 per cent concentration of carbon dioxide. When the carbon dioxide concentrations were higher than those to which the bees could adjust in a direct physiological manner, a subsidiary discriminatory and behavioral mechanism enabled the organism to survive. This mechanism was not apparent when the carbon dioxide concentrations reached a level well above that to which the honeybees might conceivably be exposed.

The third species studied, the mealworm, lives in grain where the circulation of atmospheric air is extremely limited, and the possibility of exposure to high concentrations of carbon dioxide is correspondingly increased (7, p. 99). The mealworm's behavior was apparently unaffected by 50 per cent and 25 per cent concentrations of carbon dioxide, the organisms moving freely from air to carbon dioxide and back with no evidence of respiratory distress. At the 100 per cent concentration, however, an immediate avoidance of the carbon dioxide was apparent. The above data are consistent with Gaarder's (3) report that respiration in *T. molitar* is constant while oxygen concentrations are decreased from 97 per cent to 5 per cent.

These findings generally support our hypothesis. The range of carbon dioxide concentrations to which these organisms respond is defined by (*a*) a lower threshold below which no avoidance occurs, physiological mechanisms providing adequate adjustment, and (*b*) an upper threshold above which no avoidance occurs, the likelihood of survival sharply decreasing. Our data suggest that the concentrations of carbon dioxide that arouse the avoidant response, and the concentrations where behavioral breakdown occurs, are species characteristics, determined in an evolutionary sense by the habits and habitat of the species.

Descriptions of respiration and the respiratory organs in insects fail to provide a consistent scheme for a rationalization of our results (1, 5, 8). Mealworms depend to a large extent on slow cutaneous respiration, but so do cockroaches, while honeybees are limited in this respect. In the mealworm, tracheal respiration is largely by diffusion; the honeybee depends almost entirely on forced tracheal ventilation; and the cockroach utilizes both. The rate of oxygen consumption is approximately the same in the mealworm and cockroach, but may be as much as 150 times greater in the honeybee. The huge air sacs in the respiratory system of the honeybee are not found in the mealworm or cockroach, the cockroach having small sacs, the mealworm none at all. Similarly, there are no consistent differences in the structure or function of the spiracles that can be related to our data. It seems reasonable to suspect that the basis for the species differences in response is to be found in differential nervous sensitivity to carbon dioxide.

The conception of an upper threshold, a

concentration of carbon dioxide *below* which a response occurs, requires some comment. We find in sensory physiology that extreme concentrations or intensities of stimuli may cause rapid and nearly complete adaptation of the sense receptors, giving the appearance of an upper threshold. The lack of any clear-cut evidence for the existence of carbon dioxide receptors in insects leads us to prefer an alternative view. An increase in the carbon dioxide concentration of the inspired air is rapidly followed by an increase in carbon dioxide and hydrogen ion concentration in the body fluids (5). Either or both of these increases could act directly on the nervous system resulting in a disintegration of adaptive behavior.

SUMMARY

1. This paper presents the results of an experiment testing the discrimination and preference reactions of 40 cockroaches, *Periplaneta americana*, 30 honeybees, *Apis mellifica*, and 25 mealworms, *Tenebrio molitar*, using air and carbon dioxide concentrations of 10, 25, 50, or 100 per cent.

2. Preference was defined as behavior at the choice point of a tube, one end of which was fed with air, the other end with the carbon dioxide or a carbon dioxide–air mixture.

3. Cockroaches demonstrated no ability to discriminate either the 50 per cent or 100 per cent concentrations from air, though four of ten *S*s showed a dependable preference for air at the 25 per cent carbon dioxide concentration, and all *S*s avoided the 10 per cent carbon dioxide concentration.

4. Honeybees were able to discriminate at the 25 per cent and 50 per cent, but not at the 100 per cent concentration.

5. Mealworms were capable of discriminating at the 100 per cent concentration. There was no indication of discrimination at the 25 per cent or 50 per cent concentration, but neither was there evidence of deleterious effects of these concentrations in the mealworm's behavior.

6. The possible relation of these findings to normal habitat was discussed.

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POSITIVE REINFORCEMENT OF THE BAR-PRESSING RESPONSE BY A LIGHT STIMULUS FOLLOWING DARK OPERANT PRETESTS WITH NO AFTEREFFECT

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Light stimulation is generally considered to be a strong aversive stimulus for the albino rat. Removal of light has been shown to constitute an effective reinforcement of the instrumental response in a large number of studies (e.g., 1, 2, 6, 7). To our knowledge, however, no one has reported a reinforcement function for the opposite relationship—the production of a light stimulus through some instrumental response independently of any relationship to other reinforcing stimuli.[1] It is the purpose of this report to present such evidence.

The positive reinforcing function of light stimulation here reported was first discovered in experimentation performed by Henderson (5) under the supervision of the senior author. Animals that had spent a number of days in the bar-pressing apparatus with no aftereffect accompanying their bar presses were found to show striking increments in response frequency when mild light stimuli were introduced as aftereffects of bar presses. Three further investigations specifically designed to verify this unexpected phenomenon were then carried out by us. A fourth, more extensive study was performed by Roberts (9) under the supervision of the senior author. Each of these studies involved investigation of some further variable, such as the intensity of the light stimulus. For the purpose of presenting the data in this report, however, these particular variables are ignored in order that a brief presentation may be made of the simple but important question of the efficacy of light as a positive reinforcer following nonreinforced operant pretesting. The experiments, listed in the chronological order indicated above, are summarized in Table 1.

METHOD

Subjects

The *S*s were 76 young male albino rats from the stock colony of the Department of Psychology and the Department of Agricultural Chemistry at the University of Missouri. They were distributed over the five experiments as indicated in Table 1. All but the 16 animals in Experiment 2 were experimentally naive. These 16 had had no training involving light as a stimulus or bar pressing as a response. Only those *S*s providing data directly relevant to the present purpose are included from the experiments of Henderson (5) and Roberts (9).

Apparatus

A Skinner-type bar-pressing apparatus was used. It was made of 1-in. pine stock painted a flat gray, with top and bottom composed of $\frac{1}{2}$-in. hardware cloth. Its dimensions were 5 by 6 by 8 in. An L-shaped bar, made of $\frac{1}{2}$-in. steel rod, extended into the box approximately 1 in. and was placed 1 in. above the floor. A 3- by 5-in. diffusion plate made of frosted plastic material placed between two sheets of Plexiglas constituted the top half of the box immediately above the bar. A 3- by 5- by 14-in. light box contained one $7\frac{1}{2}$- and one 15-w. bulb. This box was fitted over the diffusion plate so that the entire surface of the plate was evenly illuminated when either of the light bulbs was burning at the rear of the chamber. Temperature variations from the light were slight, with an increment of less than 2° F. occurring as a result of the steady burning of the 50-mL intensity for 30 min., with a large rat in the testing box. A pressure of approximately 20 gm., displacing the bar $\frac{1}{4}$ in., closed the contacts of a double-pole mercury dip switch, which was coated with oil to insure silent operation. In Experiment 1 the light was activated for a minimum time of 1 sec. for the test condition. Modification of the apparatus for the other experiments was made so that the light remained on as long as the bar was adequately depressed.

A battery of four such units was constructed and placed in a darkened room. Response frequencies were measured by Veeder-Root counters. These were housed in a separate room. The counters were soundproofed as a further precaution against auditory cues from their operation.

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[1] Since this report was written a similar phenomenon with female mice has been reported by G. B. Kish (A Demonstration of Learning when the Onset of Illumination is Used as a Reinforcing Stimulus. *Amer. Psychologist*, 1954, **9**, 406. Abstract). A similar recent study with rats by J. B. Girdner has also been called to our attention (An Experimental Analysis of the Behavioral Effects of a Perceptual Consequence Unrelated to Organic Drive States. *Amer. Psychologist*, 1953, **8**, 354–355. Abstract).

TABLE 1

Summary of the Experimental Conditions

Exper. No.	N	No. of Pretest Periods	No. of Test Periods	Test Light Intensity* (mL)
1	12	8	7	.024
2	16	6	12	.024, 2.44, 6.97, or 16.56
3	12	1, 3, or 9	6	.024
4	12	1, 5, or 9	6	1.18
5	24	6	9	16.56

* Intensity determinations were made with a Macbeth Illuminometer.

TABLE 2

Mean Response Increments from Last Day of Nonreinforced Operant Pretest to First Day of Test

Exper. No.	N	Mean Number of Responses		Increment	$SE_{\text{Diff.}}$	t	p
		Last Pretest Day	First Test Day				
1	12	20.9	76.7	55.8	14.09	3.96	.01
2	16	32.2	80.6	48.4	9.47	5.11	.001
3	12	23.0	37.9	14.9	5.98	2.49	.05
4	12	18.2	41.7	23.5	7.81	3.01	.01
5	24	10.6	29.4	18.8	4.71	3.99	.001
All	76	19.9	50.9	31.0	3.96	7.83	.001

Experimental Procedure

The essential procedure for all five sets of animals involved the opportunity to make nonreinforced operant responses in the dark for a varying number of 30-min. pretest periods, followed by a number of 30-min. test periods during which a relatively mild light accompanied each bar press. In the first four experiments *S*s were maintained in an environment of subdued lighting for one week prior to the beginning of experimentation and throughout pretest and test phases. In Experiment 5 (9) the nature of the pretraining environment was a major independent variable. Other procedural details for each of the experiments are shown in Table 1.

For at least one week prior to experimentation all animals were placed on a 24-hr. feeding schedule. Water was continuously available within the home cages. Pretest and test were given under $22\frac{1}{2}$-hr. hunger drive. No food reward was used at any time in relation to pretest or test. All animals were fed 30 min. after each experimental session.

RESULTS

The data here presented involve simply the question of increment in response frequency as a function of the shift from no aftereffect to a light aftereffect. The secondary variables indicated in Table 1 are not considered.

Table 2 presents the results of a comparison between the mean number of responses on the last day of nonreinforced operant pretest and on the first test day with the light aftereffect. Because of the variations of conditions among the groups each experimental group is considered separately. Large and statistically significant mean increments were found in each of the groups and for the total N of 76, as indicated in the table.

The extent to which response increments occurred as a function of the change in stimulus conditions is also demonstrated by the fact that 63 of the 76 *S*s gave such an increment. This proportion is significantly above chance (50–50) expectancy at the .001 level of confidence (chi square = 34.22, $df = 1$).

The adequacy of this criterion of chance expectancy is indicated by the fact that response scores declined from the first day of pretest and had apparently reached an asymptote by the final day.[2]

As has been indicated by previous studies of bar pressing by the rat under hunger drive (10, 11), the operant level achieved after six days of nonreinforced responding is sufficiently stable to permit sensitive tests of independent variables without the necessity of including a control group which does not receive the experimental treatment.

Comparisons of the last day of nonreinforced operant pretest with the mean of the entire series of test days also gave consistently significant results, even though there was a tendency for the response frequencies to decline over the test period.[3]

DISCUSSION

The results of the last four studies seem to provide ample verification of Henderson's original finding (Experiment 1). They indicate a strong reinforcing influence of light following operant pretest in the dark and thus substantiate the hypothesis suggested by the first result.

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[2] A table presenting all the individual data for the 76 *S*s has been deposited with the American Documentation Institute. Order Document No. 4496 from the ADI Auxiliary Publications Project, Photoduplication Service, Library of Congress, Washington 25, D. C., remitting in advance $1.25 for 35-mm. microfilm or $1.25 for 6- by 8-in. photocopies. Make checks payable to Chief, Photoduplication Service, Library of Congress.

[3] A table showing these results has also been deposited with the ADI. See footnote 2.

The possibility that the observed increment in response strength was actually due to the influence of the light stimulus per se, and not to any significant degree to the prior operant pretesting experience, must be considered. This is especially important in view of Henderson's (5) demonstration of a significant variation among light intensities as aftereffects in operant bar-pressing behavior. The stronger lights were associated with higher response frequencies up to 16.56 mL, with a reversal of this trend at the next and maximum intensity of 50.32 mL. This explanation is not supported, however, by a direct comparison within Henderson's investigation of the first–test-day results of the 12 animals reported here as Experiment 1 and another set of 12 animals. These were given the identical light stimulation (.024 mL) following responses but did not have any prior operant experience. They responded significantly less frequently on the first test day (t = 2.50, p = .05). Nevertheless, the relative roles of light per se and of prior nonreinforced operant experience in producing the increment merit further, more analytic investigation.

It is also conceivable that the results were due to some kind of unrecognized adventitious establishment of secondary reinforcing powers in connection with light stimulation. This interpretation is contraindicated by Roberts' (9) data. The smallest first–test-day increment was observed in the subgroup for which a definite attempt was made to associate light with eating behavior.

The conclusion is drawn that the present results indicate a positive reinforcing effect of light stimulation under the experimental conditions utilized. The effect here noted has been called "reinforcing" and the light stimulus a "reinforcer" in a theoretically neutral and purely descriptive sense—that is, simply to refer to the observed increment in responses associated with occurrence of the stimulus. No assumption is made as to the nature of the mechanism of such reinforcement.

Although this report is intended mainly to present an empirical account of our results, some indication of their possible theoretical significance may be made. They extend the suggestion from Henderson's study (5) that the role of light is not simply a negative reinforcing one for the albino rat, as has generally been assumed. Moreover, they suggest, as perhaps the most plausible explanation, a stimulus-change or novelty factor in response reinforcement comparable to those previously advanced (3, 4, 8). If verified under more general experimental conditions this will become an important supplement to the need-reduction interpretation of reinforcement. Whether in this case the need-reduction hypothesis can be extended to cover this kind of situation or whether a new type of reinforcing factor must be admitted constitutes a problem for further investigation.

SUMMARY

Data are presented from the bar-pressing responses of 76 albino rats to test the hypothesis that presentation of a light stimulus can reinforce an immediately preceding response following nonreinforced operant experience with that response. Statistically significant response increments under these conditions were observed in five independent sets of animals. The influence of the light per se and the possibility of adventitious secondary reinforcement effects were considered as possible explanations but rejected on the basis of available data. The results were interpreted as offering support for the positive reinforcing powers of light stimulation under the experimental conditions used and as suggesting as one possible interpretation a kind of stimulus-change or novelty factor in reinforcement.

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PLACE LEARNING WITHOUT PRIOR PERFORMANCE

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In discussing the problem of expectancy E. L. Thorndike suggested running rats through a maze in a kind of trolley car, and later testing what they had learned (3). Investigations of place and latent learning obviously have bearing upon this, but Thorndike's paradigm as such has never been followed. The present experiment was an attempt in this direction.

A total of 103 rats were drawn from one place in a room to another in a transparent cable car, all the while suffering continuous shock. After 18 such trials they were tested on an elevated T maze in three groups. For one group, the T was arranged so that the animals had to choose between running to the place where the shock started and the place where it had stopped. For the other two groups, one end of the T terminated at a "neutral" place (not associated with shock) and the other at either the "onset" or the "offset" place, respectively.

METHOD

Subjects

One hundred and three pigmented male rats from the colony at Swarthmore College were used as *Ss*. They were approximately five-months old at the beginning of the experiment and had no previous experimental training.

Apparatus

The cable cars were made of Plexiglas, 22 by 7 by 10 cm., with a wire grid floor. The back of each car was removable and served as a door through which the animal could be admitted, and it was locked afterward. These cars were suspended from a 10-ft.-long track, and were drawn from one side to the other by a pulley arrangement. The track was set up so that the cars were at the exact level of the elevated maze later used in the experiment.

The track could be set up between any two of three places, *A*, *B*, and *C*. As Figure 1 indicates, *A*, *B*, and *C* were the vertices of an equilateral triangle, and were differentiated by means of several "extra-car" cues. Screens (3 by 5 ft.) were placed directly behind these points, striped vertically at *A*, horizontally at *B*, and left unpainted at *C*. Further cues came from the home cages, and from a fairly loud buzzer placed behind *C*. The track was held up by two strong posts attached to the ceiling.

Procedure

Preliminary training. All animals were given seven days of preliminary training in another room. They were placed on a 24-hr. wet food schedule, and were trained to run down a straight elevated path with wet food as reward.

Cable car training. Four days after preliminary training was completed, the animals were divided into six training groups: (*a*) drawn from *A* to *B*; (*b*) drawn from *B* to *A*; (*c*) drawn from *A* to *C*; (*d*) drawn from *C* to *A*; (*e*) drawn from *B* to *C*; and (*f*) drawn from *C* to *B*.

These subdivisions were established in order to separate later effects due to the car training from fortuitous preferences for one particular location over another.

Every animal was given 18 trials with an intertrial interval of approximately 90 sec. except for the interval between trials 9 and 10, which was 2 hr. Each trial was conducted as follows:

At the beginning of the series the animal was locked in the cable car, where it remained for this entire period. The car was placed at the starting point, and remained stationary there for 10 sec. The car then began to move, and reached the terminus in 20 sec., where it remained stationary for another 10 sec. After this it was detached from the track and placed on the floor, directly underneath and midway between start and terminus, where it remained until the next trial began. Strong and continuous electric shock was applied 5 sec. after the animal was placed at the starting point, and was turned off as soon as it reached the terminus.

Test. Twenty-four hours after the cable car training all animals were tested under 22 hr. of food deprivation. All room cues were left exactly as they had been at the time of the cable car training, except that the track was removed. Each animal was given one test run on an elevated maze, with two arms of 5 ft. each, and a starting stem of 3 ft.

Each of the six training groups was now further subdivided into three groups:

Group I: The ends of the maze arms coincided with the starting place and terminus of the cable car trip.

Group II: The ends of the maze arms coincided with the terminus of the cable car trip and with the "neutral" place.

Group III: The ends of the maze arms coincided with the starting point of the cable car trip, and with the "neutral" place.

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[1] This study was conducted as a class project in a course in animal psychology. The writer wishes to express his appreciation to J. Burks, E. Fullager, C. Gayl, R. Grossman, M. Hill, M. Law Francis, P. Linsley, C. Montgomery, N. Newbegin, T. Stein, and B. Turlington, who conducted most of the experimental work and who contributed many valuable suggestions and criticisms.

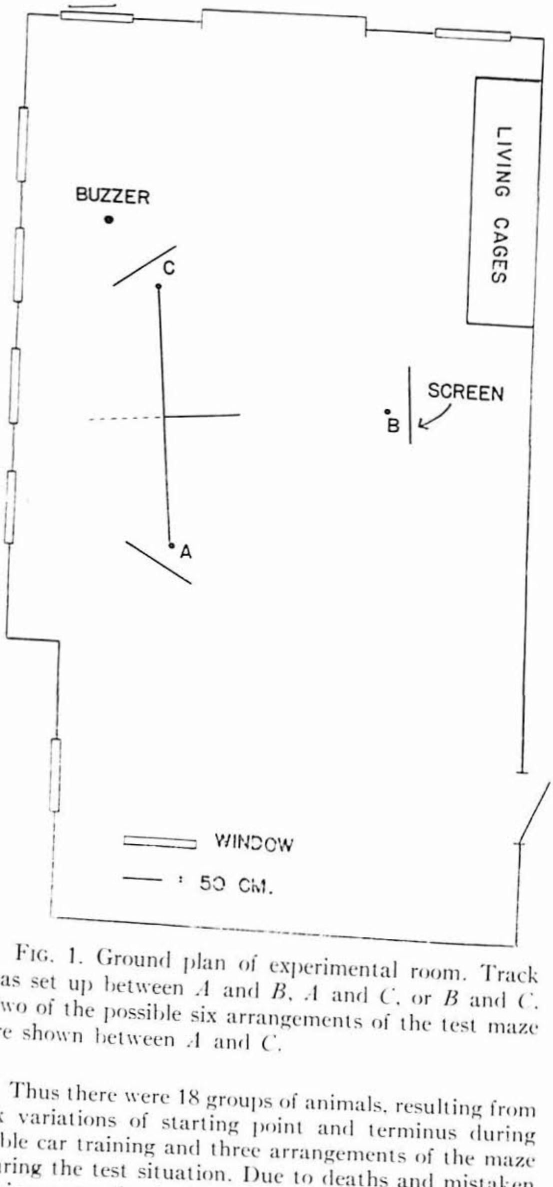

FIG. 1. Ground plan of experimental room. Track was set up between *A* and *B*, *A* and *C*, or *B* and *C*. Two of the possible six arrangements of the test maze are shown between *A* and *C*.

Thus there were 18 groups of animals, resulting from six variations of starting point and terminus during cable car training and three arrangements of the maze during the test situation. Due to deaths and mistaken assignments of animals to wrong groups, the number of cases varied somewhat from group to group. The overall design and the number of cases in each group are presented in Table 1.

TABLE 1
Number of Cases in Different Experimental Groups

Cable Car Trip During Training	Choice During Test		
	Group I	Group II	Group III
Drawn from:			
A–B	7	8	3
B–A	6	6	6
A–C	6	6	6
C–A	4	3	5
B–C	6	6	6
C–B	6	6	7

For half the animals within each of these 18 groups the starting path of the maze was arranged so that the animals started from near the center of the equilateral triangle *ABC* and moved outward to one of its sides. For the other half, the starting path was placed so that the animals started from the outside of that triangle, moving inward to one of its sides. In this fashion, possible right- or left-turning preferences were controlled.

Performance during the test trial was scored by choice, log latency, and number of VTE's made at the choice point. A choice was considered completed if the animal had traversed more than 1 ft. of one of the maze arms.

RESULTS

Since *A*, *B*, and *C* were used as starting points, termini, and neutral points for an approximately equal number of animals during the cable car training, possible preferences for particular places as such were controlled. In consequence, the breakdown of the groups by spatial arrangement of starting points and termini was ignored, and all the analysis was accomplished by testing three main groups, I, II, and III. Group I comprised all animals whose test choice was between the start and terminus of the cable car trip; Group II, those animals that had to choose between the neutral point and the terminus; and Group III, those whose choice was between the neutral point and the starting point.

The choices in all three groups are presented in Table 2. As the table indicates, there was a clear preference for the terminus on the part of those animals that had a choice between that and the starting point. Seventy-four and three tenths per cent of those animals ran towards the terminus a difference from 50 per cent which is highly significant (CR = 2.87). However, no significant preference is encountered in Groups II and III (i.e., for those animals that chose between the neutral

TABLE 2
Choice Responses During Test

	Group I Starting Point vs. Terminus ($N = 35$)	Group II Neutral Point vs. Terminus ($N = 35$)	Group III Neutral Point vs. Starting Point ($N = 33$)
Number of animals choosing:			
Starting point	9		15
Terminus	26	16	
Neutral point		19	18

point on the one hand, and either the starting point or the terminus on the other).

Analysis of the latency scores did not reveal any significant differences between the groups. The geometric mean latencies were 170.8 sec., 145.4 sec., and 136.3 sec. for Groups I, II, and III, respectively. Owing to the large variability in latencies, none of these differences even approached significance.

The mean number of VTE's were 8.91, 7.29, and 6.42 for Groups I, II, and III, respectively. An analysis of variance showed that the group effect was significant ($F = 3.404$, $p < .05$). Individual t tests yielded a significant difference between Groups I and III ($t = 2.35$), but fell short of significance for the difference between Groups I and II ($t = 1.56$), and that between Groups II and III ($t = .77$).

DISCUSSION

The choices made by Group I indicate that some place learning does occur under our conditions. The results for the two other groups, however, suggest that the "spatial map" acquired by our animals was quite narrow and confined. At first glance, the performance of these animals is rather surprising. If the animals prefer the terminus to the starting point, one would expect a differential reaction when either of these is compared with a neutral point. This expectation is reasonable *unless* the animals do not generalize extensively from one part of the room to another—i.e., *unless* they cannot recognize the starting point or terminus when regarding these from regions in the room which they had not traversed in their previous cable car training. When interpreted in this manner, our data suggest that place learning may be confined to the specific areas the animal had traversed in its previous training. To expect place performance from choice points outside of such areas would presuppose a degree of "object constancy" which the animals may not possess.

The greater number of VTE's found for Group I may be interpreted in a similar manner. More choice-point vacillation occurs for these animals because they "recognize" the region in which they were shocked.

The generality of our results may of course be questioned since electric shock was utilized. "Narrow" place learning may have been obtained, because the shock was too potent a distractor. While this is a plausible hypothesis, our results are nevertheless in line with the general findings of many studies of place learning carried out under more conventional conditions. Generally speaking, place learning seems to be obtained most readily when the animals are tested at a choice point which they have previously encountered, and when the pathways to be chosen are in areas traversed previously. Short-cut behavior (4) appears to be a much disputed phenomenon whose existence is seriously questioned (1, 2). Here the correct pathway involves a region not hitherto traversed. On the other hand, place learning is obtained very readily by *E*'s using T mazes rotated by 180° (5), where both choice point and correct path are in areas the animal is directly acquainted with.

SUMMARY

A total of 103 rats was drawn from one place in a room to another for 18 trials in a transparent cable car, all the while suffering continuous shock. They were subsequently tested on an elevated maze in three groups. For Group I, the maze was set up so that the animals had to choose between running to the place where shock began (starting point) and the place where shock had stopped (terminus). For Group II, the choice was between a neutral place and the terminus, and for Group III, between a neutral place and the starting point. Group I showed a significant preference for the terminus, but no differences were found for the other two groups. The results are interpreted as indicating (*a*) that place learning may occur without prior performance, and (*b*) that such learning is restricted to regions which the animals had previously traversed.

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CHOICE ALTERNATION: III. RESPONSE INTENSITY VS. RESPONSE DISCRIMINABILITY

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"Spontaneous alternation" is a term which has been applied to the systematic tendency of rats to choose two alternatives rather than one, when given two successive choices in a single-choice-point maze. Previous studies in this series (8, 9) have made a distinction between a "choice" and a "response," and it has been shown that of the several possible determiners of spontaneous alternation, the response has little effect.

Of the several theories which attempt to account for spontaneous alternation, the only one which seems to lead to an expectancy that the manipulation of some characteristic of the *response* would modify the tendency to alternate is that of Hull (2, 3, 4). His concept of "reactive inhibition," a negative tendency to make the response itself, has been related to this phenomenon by a number of workers. Reactive inhibition dissipates with time and is said to be an increasing function of the amount of work involved in making the response. That spontaneous alternation varies with the amount of time between choices is undisputed. That it varies with the amount of work seems questionable.

Montgomery (5) placed levers at the ends of the arms of a T maze and varied the weights on the levers in order to vary the amount of work involved. The amount of work did not influence the degree of alternation. Solomon (6, 7) strapped various weights to rats and observed that variation in the amount of weight did not lead to variation in the amount of spontaneous alternation. Solomon (6, 7) did, however, find that when the amount of work involved was varied by inclining the goal stems of an elevated maze by 16°, the increased work seemed to lead to a greater tendency to alternate.

The two experiments to be reported here were designed (*a*) to vary the amount of work by increasing the incline of the enclosed T maze to 45° in an effort to maximize the effect Solomon observed, the "Response Intensity" experiment, and (*b*) to vary the quality of the response by forcing the rat to twist its body quite sharply in the direction of the choice, the "Response Discriminability" experiment.

The rationale for the first experiment needs no further explication, perhaps, but that for the second might be extended somewhat further. The previous studies seemed to support the conclusion that the tendency to alternate with respect to the intramaze stimuli, for example, is a function of the discriminability of the two sets of stimuli. If the two goal stems are quite similar in color, shape, shadow, and texture, alternation will be at a minimum. If this generalization is extended to the response, and if the nature of the afferent feedback from the response is considered a relevant stimulus, then the following expectation results. If the afferent feedbacks from the two responses, turning left and turning right, are very similar in nature and thus not highly discriminable, alternation with respect to the response will be at a minimum. Variations in work should lead to variations in the intensity of the feedbacks from the two responses, but would not be expected, under most circumstances, to make much change in the discriminability of the two feedbacks. The operation of forcing the rat to twist sharply in three dimensions during choice was the best operation we could think of for insuring that the afferent feedbacks from the two responses were highly discriminable, and we reasoned that this operation should lead to a marked increase of the importance of the response as a determiner of alternation.

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[1] The data of Experiment 1, "Response Intensity," were collected by Mr. Fawl for his honors thesis for the A.B. degree. Mr. Fawl is now at the University of Kansas.

The apparatus for Experiment 2, "Response Discriminability," was designed and built and the data were collected by Mr. Earl. This study was supported in part by a grant from the Horace Rackham School of Graduate Studies and in part by a grant from the National Science Foundation.

METHOD

Subjects

Experiment 1—Response Intensity. Eighteen male albino rats which were experimentally naive were used in this experiment. They were purchased from a near-by medical supply source, and although the birthdate was unknown, they were approximately four months old at the beginning of the experiment.

Experiment 2—Response Discriminability. In this experiment 28 animals were given preliminary handling. Two were discarded on the first day of the experiment because they would not leave the starting box, and 2 were not started since the design called for 24 animals. This group consisted of naive male albinos from the University of Michigan colony; all were born on the same day, and were seven months old at the beginning of the experiment.

Apparatus

Experiment 1—Response Intensity. This was the familiar +-shaped maze with both a north and south entrance. It was used as a T maze from either direction. The starting stems were painted gray, and one goal arm and box were black and one white. The floor of the starting stems had hardware cloth which was 3 wires to the inch, one goal arm floor was 2 wires to the inch, and the other was 4 wires to the inch. Other dimensions have been described previously (8).

One important modification of the standard maze was made. The goal arms were hinged in such a way that the first 12 in. of each goal arm could be inclined to an angle of 45°, which raised the goal boxes slightly over 8 in. higher than the starting stem. Guillotine gates were installed so that the animal could be retained on the incline for a given period before it was permitted to proceed to the goal box. By confining the animal in this section of the maze for 20 sec. on each trial, the time spent in this portion could be equalized for inclined and level positions of the maze.

Experiment 2—Response Discriminability. A newly built maze was used in this experiment which was similar to the +-shaped maze used in earlier studies (8, 9), and was a close reproduction of the maze used in Experiment 1, except that an effort was made to make the afferent returns from the response as different as possible between the two alternatives.

The two goal alleys were raised on stilts so that the floors of each goal wing were on the same level and at the same time stood 7½ in. above the floors of the starting alleys. Inclined ramps were built at the choice points so that the rat could climb from the level of the starting alley to the higher level of the wings of the goal alleys. In this manner a clover-leaf intersection was formed, and each ramp was banked steeply like the turn of a race track or the end zone of a stadium. The four ramps were symmetrical with respect to radius, bank, and grade of the incline. The incline commenced before the choice point, and the floor sloped away from the mid-line of the starting alley. Thus the rat straddled a ridge at the choice point, and both the bank as well as incline could be sampled by the rat prior to its choice. This maze was painted gray throughout, but black and white metal inserts were made which permitted lining the walls and slipping a colored insert under the floor from the beginning of the choice point to and including the goal box. One alternative was black and one was white. The hardware cloth floor of this maze was a uniform three wires to the inch throughout.

Procedure

The animals in both experiments received prehandling. In Experiment 1 they were handled and hand-fed for a week before the first experimental day. In Experiment 2, they were run on boards between chairs for four days.

The running procedure was approximately the same for both experiments. The animals were transported from the colony to a position outside the experimental room and were taken one at a time into the room and given two trials. They were confined briefly in small individual cages between trials while the maze was being adjusted. When all animals had been run, they were returned to the colony room and fed their daily ration of approximately three Purina Laboratory Chow pellets about 1 hr. after running. Thus, at the time of running, the animals were approximately 22 hr. food-deprived, and they received no food in the maze.

Experiment 1—Response Intensity. In the original design six conditions were planned and run. Two conditions were subsequently added. One original condition involved starting the animals at the same place twice with the arms level. This condition was replicated from the other starting stem. This is the standard alternation phenomenon procedure. The third and fourth conditions were identical with the first and second except that the goal stems were raised to the inclined position in order to permit observation of the effect of increased work. The last two conditions involved starting the animals first at one starting point and then at the other to permit the separate assessment of the effects of stimulus and response as in the Montgomery (5) and Glanzer (1) experiments. The animals were run through the experiment in groups of six. Each of the six animals experienced all six conditions in six days, and on each day, each of the animals within a group was experiencing a different condition.

Because of the nature of the results obtained in the above conditions, two additional conditions were run several weeks later in which the animals were started on the two trials in opposite starting stems and the goal alleys were inclined. Unfortunately, 3 animals had contracted "sniffles" in the meantime, and only 15 were run in these conditions.

Experiment 2—Response Discriminability. In this experiment the design was identical with that executed in the first experiment reported in this series (8). There were eight possible conditions, with all conditions being run with the inclined and banked ramps in place. When started twice from the same starting position, the animal was required to alternate stimulus, place, and response or repeat all three. There were two such conditions since there were two possible starting positions. A second pair of conditions involved starting the animals from one starting arm on the first trial and the other starting arm on the second. Thus, stimulus and place were pitted against response. The fifth and sixth conditions consisted of starting the animals twice from the same position in the room, but rotating the maze 180° between trials. These two conditions pit response and place against stimulus. The last two conditions consist in starting the animals first from one position in the room, then the other, with the maze rotated 180° between trials. These two conditions pit response and stimulus against place.

The animals were divided into eight groups of three animals each. Each group was run under a different one of the eight conditions each day, and each group was run through all eight conditions once for a total of eight running days.

TABLE 1

Relative Tendencies to Alternate in Each of the Conditions of Experiment 1, the "Response Intensity" Experiment

Alternation Choice	Average Number of Alternations Per Animal	Total Number of Alternations in Group	Percentage of Alternations
	Maze Level		
Stimulus and response	1.83 (a)	33	91.7
Nothing	0.17	3	8.3
Stimulus	1.00 (c)	18	50.0
Response	1.00	18	50.0
	Maze Inclined		
Stimulus and response	1.61 (b)	29	80.6
Nothing	0.39	7	19.4
Stimulus	1.53 (d)	23*	76.7
Response	0.47	7*	23.3

Comparison	*t* †	*p*
a–b	1.47	n.s.
a–c	5.68	.001
a–d‡	1.84	.10
b–c	2.37	.05
b–d‡	0.91	n.s.
c–d	2.24	.05

* Three animals had contracted cases of "sniffles" before this condition was run. Consequently, the *N* for this condition is 15 instead of 18.

† These *t* values were obtained by using the formula for testing the significance of the difference for correlated means. See the earlier study (8) for a discussion of this problem. There are 17 *df* available for comparisons involving a, b, and c. There are only 14 *df* for the three comparisons involving d. The means used in testing d comparisons with a, b, and c were slightly different from those reported in the table, since the scores of three animals were removed for these comparisons.

‡ Two differences are testable in these comparisons. For example, in the a–d comparison, one may test whether 1.83 is significantly different from 1.53, or whether it is significantly different from .47. The smaller difference is significant at only the .1 level, while the larger difference would be highly significant. The same is true of the b–d comparison, where the smaller difference is tested and found not significant, while the larger one (1.61–.47) would be highly significant.

RESULTS AND DISCUSSION

The first of this pair of experiments was designed to try to magnify the increased alternation Solomon (6, 7) observed when he inclined the arms of an elevated maze by 16°. In this experiment in an enclosed maze, the arms were elevated 45° and the animals were detained on the incline for 20 sec., which made a further increase in the amount of work involved. The results may be seen in Table 1. With the maze in the level position and the animals started twice from the same position, 91.7 per cent alternation was observed. When the maze arms were inclined and the amount of work was thus increased considerably, the tendency to alternate dropped to 80.6 per cent. This finding is the reverse of what would be expected if increased work increased the tendency to alternate. In this instance, increasing the amount of work *decreased* the tendency, although the difference is not statistically significant.

When the animals were started first from one starting stem and then from the other in an attempt to replicate the findings of Glanzer (1) and Montgomery (5), half the responses were alternations of stimulus and the other half were alternations of response. In a similar situation the above authors have found stimulus all important and response of little or no consequence.[2]

Some aspect of the situation which had not been anticipated operated to decrease the effectiveness of the stimulus or to increase the effectiveness of the response with the maze in the level position. We cannot yet state with any assurance what that variable might have been. We did reason, however, that since an increase in effort had produced a reduction in alternation or an increase in the tendency to repeat the response in the standard condition, running the animals first from one stem and then from the other with the arms inclined might be expected to again increase the

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[2] This experiment was actually carried out in 1951, much earlier than the later positive replication of the Glanzer and Montgomery results reported in the first experiment in this series by Walker, Dember, Earl, and Karoly (8).

TABLE 2

Relative Tendencies to Alternate in Each of the Situations Provided by the Design of Experiment 2, the "Response Discriminability" Experiment, as Compared with the Results Obtained in the Study by Walker, Dember, Earl, and Karoly (8)

Alternation Choice	Nondistinctive Response (8) Average Number of Alternations Per Animal	Nondistinctive Response (8) Total Number of Alternations in Group	Nondistinctive Response (8) Percentage of Alternations	Distinctive Response Experiment 2 Average Number of Alternations Per Animal	Distinctive Response Experiment 2 Total Number of Alternations in Group	Distinctive Response Experiment 2 Percentage of Alternations
RPS	3.08 (a) (1.50)* (1.58)	74	77.1	1.87 (w)	45	93.7
O	.92 (.50) (.42)	22	22.9	.12	3	6.3
PS	3.04 (b) (1.50) (1.54)	73	76.0	1.04 (x)	25	52.1
R	.96 (.50) (.46)	23	24.0	0.96	23	47.9
RP	1.83 (c) (.79) (1.04)	44	45.8	1.04 (y)	25	52.1
S	2.17 (1.21) (.96)	52	54.2	0.96	23	47.9
RS	2.33 (d) (1.17) (1.17)	56	58.3	1.54 (z)	37	77.1
P	1.67 (.83) (.83)	40	41.7	0.46	11	22.9

Comparison	t†	p
w-x	4.03	.001
w-y	4.97	.001
w-z	2.31	.05
x-y	0.00	—
x-z	2.31	.05
y-z	2.40	.05
a-w	2.70	.01
	2.13	.05
b-x	2.07	.05
	2.27	.05
c-y	1.18	n.s.
	0.00	n.s.
d-z	2.01	.05
	2.01	.05

tendency to repeat the response and thus alternate the stimulus. The 15 animals run under these conditions performed as predicted and now yielded results in the direction of those obtained by Glanzer and Montgomery, in whose experiments effort was not a variable.

While this experiment is much less clean and satisfactory than one might like, it at least seems to demonstrate that an increase in work and thus an increase in the intensity of the afferent feedback from the response does not lead to an increase in the tendency to alternate.

Experiment 2 was designed to be as nearly like the first experiment of this series (8) as it was possible to design it, but at the same time to maximize the qualitative differences in the afferent feedbacks from the two responses with the amount of work involved in the two responses held as constant as possible. We reasoned that if the response could thus be made a factor in the determination of the tendency to alternate, the various comparisons made in the first study in this series would now show a response effect which would show up very much like the shifting of an additional weight back and forth on the two pans of a balance scale. The effectiveness of this conception may be seen in the results presented in Table 2, where they are placed beside the results of the Walker, Dember, Earl, and Karoly experiment for comparative purposes. It can be said that in each comparison, the addition of a distinctive difference between the two responses has increased the effectiveness of the response in producing alternation. When the animals are permitted to alternate the stimulus, the place, and the response simultaneously, 93.7 per cent of their second choices were opposite from their first. When in order to alternate with respect to stimulus and place together it was necessary to repeat the response, this percentage dropped to 52.1. In other words, 47.9 per cent of the animals chose to alternate the response and to repeat the stimulus and place of the first choice. Many comparisons of the relative effectiveness of the three possible determiners of alternation are possible within this experiment, and others involve comparison with the earlier experiment. They seem to show quite clearly that the operation of making the response discriminable increased the effectiveness of the response as a determiner of alternation from practically nothing in the early study to practically equal effectiveness with the stimulus in the present study. The two experiments reported in this paper taken together seem to permit the conclusion that since it is response quality and not response intensity which influences choice alternation, Hull's concept of reactive inhibition, without considerable modification, is inapplicable to studies of spontaneous alternation.

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* In the first experiment of this series (8) the animals were run through the entire design twice, and since each major condition was tested twice within the design, an animal could make an alternation score of 0, 1, 2, 3, or 4. In the present study on "Response Discriminability," the animals were run through the design only once, and could thus score 0, 1, or 2. In order to permit comparisons between the two experiments, two means were calculated, one for each replication of the design in the "Nondistinctive Response" experiment. These two means are in parentheses. In the comparisons between these two experiments, these two means yield two independent tests of each difference.

† The t values involving only w, x, y, and z were obtained by testing for the significance of the difference between correlated means with 23 df. The t values involving comparisons between a, b, c, and d against w, x, y, and z were obtained by using the formula for testing the difference between uncorrelated means with 46 df.

Some brief word should be said about the importance of these studies for psychological theory in general. It seems to the senior author that much of learning theory and for that matter psychological theory in general concerns itself with situations which can be described as producing variability in behavior and subsequent reduction in variability as the function of the operation of variables described as rewards, need reductions, tension reductions, closure, stimulus reductions, etc. Much attention has been paid to the nature of the variables producing reductions in variability, but relatively little attention has been paid to the variables influencing the variability in behavior which is subsequently to be reduced.

A single-choice-point situation where the organism exhibits no great preference for either of the alternatives is in some respects ideal for the study of variability. The choice acts like a knife edge balance. A small decrement in a response tendency which could not otherwise be observed is detected by a reversal in the "greater than–less than" relationship. It is limited chiefly by the binary character of the data and by the limitations in the variables which can be manipulated.

Because of the nature of the variables available for manipulation, our work has led us to consideration of characteristics of afferent inputs and to differences between the afferent inputs relevant to two elements of a choice situation. We think, now, that we can make some limited generalizations about what might be expected to influence the degree of variability in behavior in such a situation.

It seems clear that the greater the discriminability of the two afferent inputs corresponding to the two alternatives, the greater the tendency to alternate.

It also seems clear that simultaneous increases or decreases in the amount of work involved in a choice and thus the intensities of the afferent inputs should not contribute to alternation.

The decremental effects of afferent inputs should dissipate with time.

Many problems remain. The most intriguing ones, perhaps, involve the general question, "When are two choices to be regarded as the same choice?" We found that exposure to stimulus and place without the rat's making a choice did not influence the choice. Therefore, exposure is not enough. The organism in some sense must make one choice before a subsequent choice is influenced. We know that successive choices in a tandem maze where the choices seem very much alike to E do not seem to be the same choices to the rat, as evidenced by the degree to which one choice influences a subsequent choice. Along which dimensions of sameness or differentness may choices be arrayed, or which sets of choices will fall in the category "same" and which will fall into the category "different" remains to be seen.

Elementary textbooks tend to describe the variability which is reduced by reward as *random*. Many Es who take a 50 per cent choice performance as a basis for showing a difference also make the implicit assumption that the behavior at 50 per cent choice is *random*. The full weight of the studies reported in this series, along with the rather large body of data reported by other investigators, seems to argue that variable behavior is often, if not always, *systematic*.

Empirically, in spontaneous alternation we are dealing with a decrement in a behavioral tendency. If our findings have generality, we might expect this class of decrement to have something in common with other well-known decrements. Some of these might be binocular rivalry, oscillations of figure-ground relationships in ambiguous figures, flicker-fusion frequency, and probability biases in choice patterns. Exploratory behavior might possibly be derived from a neural mechanism designed to account for the decrements observed in this series of studies. If these rather lengthy extrapolations have any merit, it would be expected that the variables applicable to spontaneous alternation—the positive effect of discriminability, the negative effect of intensity, the decrease in the tendency with time, and any other discernible variables—should be to some degree applicable to the other instances of decrement. At least the derivative consequences are experimentally testable.

SUMMARY

Two experiments in choice alternation are reported in which an attempt is made in one experiment to vary the work involved in the choice and thus vary the intensity of the afferent feedback from the response, and in the second experiment an attempt is made to vary the discriminability of the afferent feedbacks of the two responses by requiring differential physical contortion at the choice point.

Eighteen white rats were used in the first experiment and 24 in the second. Both experiments utilized a +-shaped maze which could be used as a T maze from opposite starting stems. The first design permitted separation of the contribution to the determination of alternation of stimulus and response, while the second permitted separation of the effects of stimulus, place, and response, or afferent input from the inside of the maze, the outside of the maze, and the inside of the animal.

Increasing the work or effort involved in making the response did not lead to an increase in the tendency to alternate, as would be expected from Hull's concept of reactive inhibition. What effect there was of increased work was in the reverse direction—increases in the tendency to repeat the response. Increasing the discriminability of the alternatives with respect to the response produced a large increase in the tendency of the response to play a positive role in the production of alternation.

The phenomenon of choice alternation is treated as a basic manifestation of variability of behavior, and variability treated as propaedeutic to selective learning. Implicit is the assumption that variability in behavior should not be treated as being random, but should be considered as a systematic pattern of behavior. The expectation is expressed that the extent to which these findings are generalizable to other instances of behavioral decrement—binocular rivalry, ambiguous figure fluctuation, flicker-fusion frequency, probability bias in choice patterns, and exploratory behavior—will be tested by the extent to which the same variables seem to operate in each of these very different situations.

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PERSISTENCE OF PERFORMANCE DIFFERENCES ON DISCRIMINATIONS OF VARYING DIFFICULTY[1]

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It was known when the present experiment was begun that simple discriminations were eventually learned by monkeys in a single trial or in very few trials (2), and it was hypothesized that the solution of more difficult discriminations would attain or approach an equal level of efficiency if a long series of problems were presented. Difficult discriminations differ from the simple only in the smaller number of available cues, the smaller amount of differential stimulus surface, or in lesser differentiability of cues. It was presumed that the monkeys would learn to use the available cues and that this perceptual learning process would show interproblem transfer, i.e., the animals would progressively improve in their facility to differentiate limited stimulus cues. As a result, the differences in learning rates on individual problems should disappear and the asymptotes of performances for the more difficult discriminations should approach or become identical with those of the simpler.

Such a hypothesis would be in keeping with Hebb's theory of perceptual acquisition (5); indeed, if the ready perception of stimulus detail is learned, it is almost certain that interproblem transfer takes place. Thus, the present experiment was designed to test the hypothesis that monkeys will learn to differentiate stimulus cues with progressively greater facility during the course of interproblem learning, and as a result performance on difficult and simple discriminations will become progressively more similar.

METHOD

Subjects

A total of 16 young rhesus monkeys served as *Ss* in this experiment. Six of these animals, no. 174, 178, 179, 181, 184, and 187, were tested initially, and the other 10 animals, no. 182, 200, 201, 202, 203, 205, 206, 207, 208, and 209, began the experiment 32 days later. The previous laboratory experience of all these *Ss* was very similar. Both groups had had extensive taming and test cage adaptation, and both had participated in similar partial reinforcement problems (8) in which they had responded by displacing a single 3-in. wooden block. Preliminary to the present experiment, all 16 monkeys were trained to displace a single 3-in. by 3-in. white card placed over the single food well of a test tray. The *Ss* were given 50 trials per day on this prediscrimination training, and in seven to ten days all attained a criterion of 90 per cent responsiveness during 10-sec. trials.

Apparatus

The animals were tested with the Wisconsin General Test Apparatus, which consists of a restraining cage and an adjoining table which supports a tray carrier and test tray, and two screens, a forward opaque screen and a rear one-way–vision screen. A detailed description of the apparatus has been given elsewhere (4). A gray test tray with a single, centered food well was used in the preliminary testing, and a gray test tray with two food wells separated 12 in. center to center was used in the experiment proper.

The stimuli were 3-in. by 3-in. cards of heavy white posterboard on which colored squares were centered. The entire surface of the stimuli was sprayed with clear plastic to permit cleaning. The colored squares varied in texture (e.g., construction paper, terry cloth, satin, painted paper, etc.), color (including hue, saturation, and brightness differences), and area. Four color-area conditions were used: 12.5, 25, 50, and 100 per cent of the surface of the cards. On each particular problem, color was the only differential cue; area and texture of the colored squares were identical for both members of the stimulus pair. Figure 1 illustrates the four color-area conditions.

Individual Trial Procedure

At the beginning of each trial, *E* lowered the opaque forward screen, baited the appropriate food well with a raisin or peanut, and centered the stimuli over the food wells. The one-way–vision screen in front of *E* was then lowered, the forward screen raised, and the tray pushed toward *S* in two distinct motions separated by a 1-sec. pause when the tray was just out of *S*'s reach. After the card was displaced and the reward taken if the choice was correct, the tray was withdrawn and the one-way–vision screen raised. The forward screen was then lowered, and, after *E* had recorded the response, the next trial was initiated. A noncorrection technique was used throughout.

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[1] This research was supported in part by the Research Committee of the Graduate School from funds supplied by the Wisconsin Alumni Research Foundation and in part by a grant to the University of Wisconsin from the Atomic Energy Commission Contract No. AT (11-1)-64.

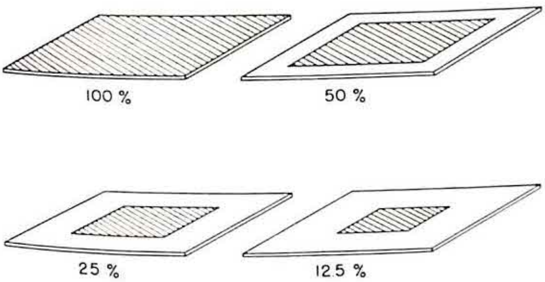

FIG. 1. Stimuli representing the four color-area conditions.

Experimental Design

The *S*s were tested for 64 days during which they received a total of 768 problems, 192 problems in each of the four conditions of color-area. Twelve six-trial problems, three from each of the four conditions, were presented daily. The daily problem sequences were drawn from permuted 4 by 4 latin squares, thus insuring the presence of each of the four conditions in each third of the sequence. The original 16 sequences drawn in this manner were randomly reordered for the remaining 48 test days.

This design made possible an analysis of variance in which animals, blocks of days (four 16-day blocks), and conditions of differential color-area were the main effects.

Arrangement of Stimuli

Two identical sets of stimulus cards were made to guard against the possible destruction of cards by the animals. Each set consisted of 400 cards and included a multiplicity of color-texture combinations in all four color-area conditions. The sets were paired identically, forming two sets of 200 pairs. The cards were paired randomly except for the restrictions that both members of a pair must be alike in color-area and texture and dissimilar in color. Because 192 of the 200 unique pairs were used in each 16-day period, repairing was necessary at the end of that time and was accomplished by repeating the above procedure. The members of each pair were randomly designated as correct (rewarded) or incorrect (nonrewarded), and the right-left position of the rewarded card was determined by following a set of positional sequences previously developed by Harlow (3).

RESULTS

The results, as indicated by analysis of variance of the performance of the 16 monkeys on successive 16-day blocks, are summarized in Table 1. Grouping of the scores of all 16 *S*s was justified by the use of Bartlett's test of homogeneity of variance (1), which yielded a corrected χ^2 value of .915 with $p > .30$.

The *F* ratios for main effects indicate significant variation among animals (individual differences), problem blocks (learning), and color-area conditions (effect of the four areas of differential color). The animals × blocks interaction (individual differences in rate of learning) is significant, while the animals × conditions interaction (consistent individual performance on conditions) is not. The blocks × conditions interaction (effect of color-area conditions on learning) is significant; inspection of Figure 2, which shows orderly separation of the curves for the various conditions on the last three problem blocks, indicates that the variation on the first problem block is responsible for this significant *F* value. First-order interactions were tested against the second-order interaction, and main effects were tested against the appropriate significant first-order interaction. All significant effects were demonstrated by $p < .001$.

The significance of the variation in performance among the four color-area conditions was tested by means of the Tukey Gap Test (10). Despite the low power of this test for quantitatively varying factors, it separated all means of the four area conditions at the .01 level of confidence.

Performance on successive problem blocks with the four color-area conditions as parameters is plotted in Figure 2. The curve for the 12.5 per cent condition appears linear and the curves for the other conditions appear progressively less linear and more negatively accelerated. The nature of these curves, in keeping with the significant *F* ratio for the problem blocks in the analysis of variance, gives ample evidence of the formation of learning sets for all four conditions of differential color-area. The graph also reveals that inter-

TABLE 1

Summary of Analysis of Variance

Source	*df*	Sum of Squares	Mean Square	*F*
Animals	15	98,314.2	6,554.3	14.16**
Blocks	3	147,939.6	49,313.2	106.53** (A × B)
Conditions	3	16,232.6	5,410.9	23.04**
A × B	45	20,832.1	462.9	6.16**
A × C	45	3,433.0	76.3	1.02
B × C	9	2,114.0	234.9	3.13**
A × B × C	135	10,140.1	75.1	

** Significant at the .001 level of confidence.

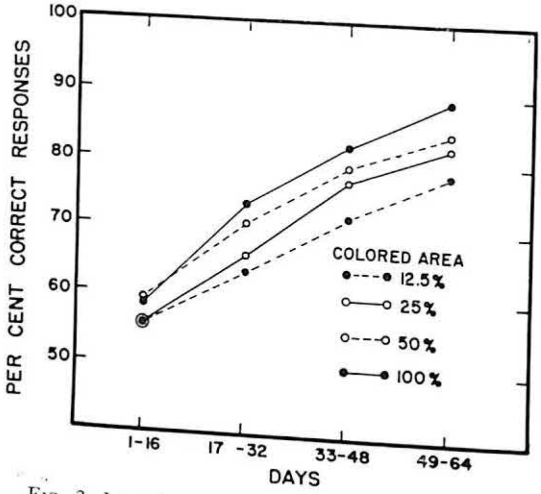

FIG. 2. Learning set curves for the four color-area conditions based on trials 2 to 6.

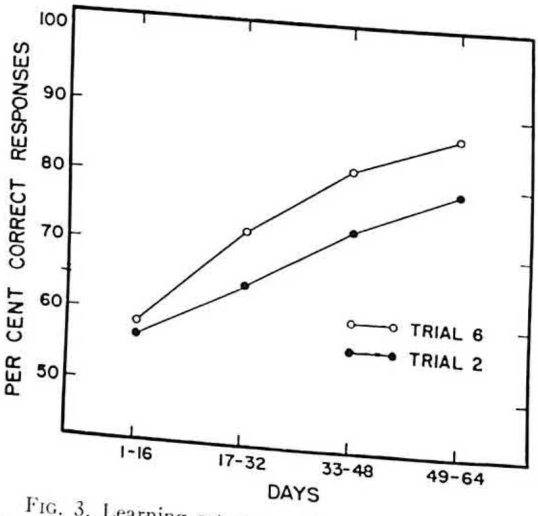

FIG. 3. Learning set curves for trial 2 and trial 6 for all color-area conditions combined.

condition differences increase after the first block of problems and then stay relatively constant during the 64-day span of the experiment.

Figure 3 shows curves which group responses on all color-area conditions plotted as a function of problem blocks with trials 2 and 6 as parameters. The trial 2 curve appears linear, and the trial 6 curve shows a trend toward negative acceleration. Differences between the curves are initially small and increase subsequently.

DISCUSSION

The most striking result of the present investigation was the failure to substantiate the hypothesis that the learning rate on individual problems and the terminal level of performance for the more difficult discriminations would approach those of the simpler discriminations. In spite of the fact that the animals demonstrated effective learning set formation for all four degrees of discrimination difficulty, differences attained constancy and gave no indication of diminishing.

If the monkeys had learned to respond visually to the locus of the differential portion of the stimuli, it would be expected that performance on the four conditions would have approached a common asymptote. The fact, however, that the curves maintained a constant amount of separation over the course of the last 576 problems gives strong presumptive evidence of failure within a reasonable time to learn to attend with increasing efficiency to the differential area of the stimuli. Thus, if the monkeys learned a "response of discriminating" as suggested by Reid (9), or if they acquired Wyckoff-type "observing responses" (11) adequate to permit efficient solution of the difficult problems, or if the color cue "acquired distinctiveness" (Lawrence 6, 7), the effect of these processes was not sufficient to overcome that of the difficulty level imposed by differences in cue level.

It seems obvious that the ability of the developing primate to respond efficiently to small detailed stimuli is a function of learning, but the nature of the conditions making possible this efficient learning to observe has not yet been adequately described.

SUMMARY

Sixteen naive rhesus monkeys were tested on a total of 768 six-trial problems in which the animals were required to discriminate between differentially colored squares mounted on otherwise identical 3-in. by 3-in. white cards. Four conditions of differential color-area were employed: 12.5, 25, 50, and 100 per cent of the surface of both stimuli used in any problem.

The results of this experiment reveal significant interproblem learning and demonstrate learning set formation for problems ranging in degree of difficulty. The significant differences in performance between all differential color-area conditions, however, indicate that discrimination difficulty is inversely related to the extent of differential color-area. During the

last 576 problems the differences in performance among the various categories did not decrease with practice, and there was no indication that they were approaching a common asymptote.

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DISCRIMINATION LEARNING PERFORMANCE UNDER DIFFERENT FIRST-TRIAL PROCEDURES[1]

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An earlier investigation of the effects of differing first-trial procedures upon discrimination learning performance has been reported (3). In that study, four groups of monkeys were trained on a series of 250 object-quality discrimination problems. The groups differed only according to whether the animals in each group found food, no food, or a marble on the first trial of each successive problem. Marked differences among the groups were found in initial performance, in interproblem learning, and in the relative importance of correct and incorrect initial preferences in a series of test problems. The present experiment extends the previous investigation to additional groups involving new first-trial procedures. Since the background, procedures, and results of the present study closely relate to those previously reported, familiarity with that account will be assumed in order to achieve maximal brevity in this report. The present experiment extends the previous one by (*a*) reversing the usual role of reward or its absence, and by (*b*) simultaneously pairing a presumably nonrewarding signal with a rewarding one.

METHOD

Subjects and Apparatus

Twelve naive rhesus monkeys participated in the experiment. All were tamed and trained to displace a single object from a food well to secure food.

The entire experiment was conducted in a modified version (2) of the Wisconsin General Test Apparatus (1), using procedures reported elsewhere in detail (2). Essentially, the animal displaced one of two simultaneously presented stimulus objects from a food well to obtain food (trials 2 through 6). The noncorrection procedure was used throughout.

Procedure

Each problem lasted only six trials. As soon as one problem was completed, a new one was introduced. Ten problems were administered daily for 30 days. The first 25 days constituted Phase I and the remainder Phase II of the experiment. Treatment differences among the groups were maintained throughout the 250 problems of Phase I, but during Phase II (50 problems) all groups were treated alike.

The 12 animals were assembled into four groups of 3 animals each. Differences among the groups involved only the first trial of each problem. On trials 2 through 6 of each problem all animals were treated alike.

Group No Food (+). No matter which object the monkeys chose on the first trial, they uncovered an empty food well. This choice, however, defined the "correct" object. Its selection, and only its selection, could secure food for the animals on subsequent trials.

Group Food and Marble (+). No matter which object was chosen on trial 1, its removal from the food well uncovered food reward and a marble. This choice also determined the correct object of the problem, and its selection on subsequent trials secured food, and only food, for the animals.

Group Food (−). These monkeys found food under the object of choice. Nevertheless, to secure food on trials 2 through 6 they had to select the other member of the stimulus pair.

Group Food and Marble (−). The animals of this group, like those of Group Food and Marble (+), invariably uncovered food and a marble on trial 1. Unlike that group, however, the members of Group Food and Marble (−) had to select the other (nonpreferred) object on subsequent trials to secure food. In this respect their obligations were similar to those of Group Food (−).

In Phase II of the experiment all animals were administered 50 problems. Like the procedures in effect during Phase I, six trials were allowed for each problem, ten problems per day. Unlike the procedures of Phase I, however, all animals on all trials of all problems found food under the correct object and no food under the incorrect object. These procedures thus agreed in every respect with those employed on trials 2 through 6 of the problems given in Phase I. The net effect of these procedures was to make the success of the response on trial 1 determined by chance. The animals had to discover which object consistently covered food.

RESULTS

The four panels of Figure 1 show intraproblem learning curves for each of the groups by successive blocks of 50 problems. The following observations can be made regarding this figure. (*a*) Confirmation of a preference by food and marble (Group Food and Marble [+]) or by an empty food well (Group No Food [+]) results in relatively flat intraproblem learning curves, whereas in-

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[1] Supported in part by a research grant (M-589) from the National Institute of Mental Health of the National Institutes of Health, U. S. Public Health Service.

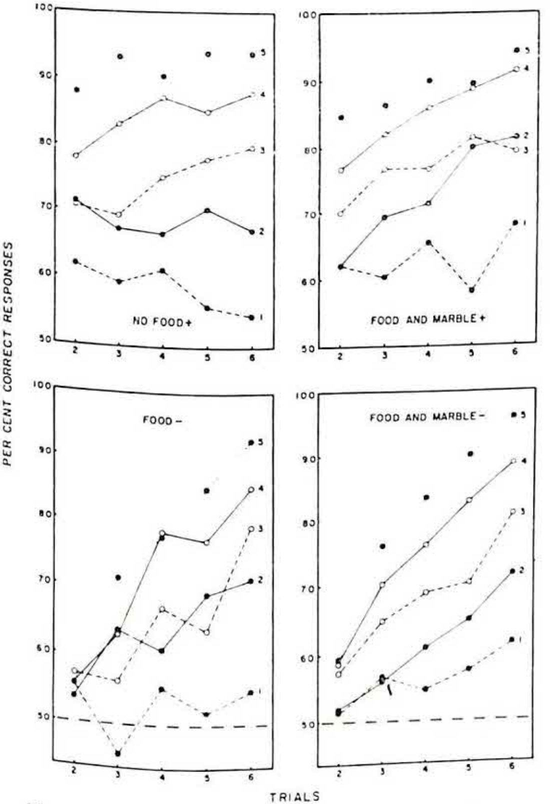

FIG. 1. Intraproblem learning curves for each group based on five successive blocks of 50 problems each.

firmation of a preference, either by food and marble or by food alone, results in progressive steepening of the curves. (*b*) Confirmation of a preference by either of the procedures applied to the two (+) groups is as effective as is the other procedure. (*c*) Intraproblem learning curves for all groups are approximately horizontal and near chance level during the first 50 problems. (*d*) Although the procedures for Group Food (−) and for Group No Food (+) are equivalent in that both signals contradict their counterparts on trials 2 through 6, the successive intraproblem learning curves for the two groups become increasingly dissimilar from the first to the fifth block of 50 problems.

These observations are supported by the analysis of variance,[2] particularly the interaction of *Trials*, *Problems*, and *Groups* based on 48 *df*. This variance estimate was significant beyond the .01 level of confidence when tested against the *Trials* × *Problems* × *Animals within Groups* interaction term based on 128 *df*.

In Figure 2 are shown interproblem learning curves (learning set curves) for trials 2 and 6 for each group. Inspection of the left panel reveals two distinct families of curves for trial 2. The two (+) curves rise continually, whereas the two (−) show little, if any, real elevation within the 250 problems. In the right panel of this figure are shown curves for trial 6. In contrast to the differences found for the trial 2 curves, these curves follow essentially similar courses. Whatever real differences may exist, they are found during only the early phases of the experiment.

Performance on the problems administered during Phase II is reflected in the curves in the four panels of Figure 3. The 50 problems given to each group have been divided into two approximately equal classes: those in which the initial response was correct, and those in which the initial response was wrong. The dashed curves refer to performance on trials 2 through 6 following a correct initial choice, and the solid curves refer to performance following an incorrect initial response. The following interpretations may be drawn from this figure. (*a*) For the two (+) groups, performance on trial 2 following a correct initial choice is superior to that following an incorrect initial choice, whereas the reverse is true for the Food (−) and the Food and Marble (−) groups. (*b*) Animals of Group No Food (+) made only 14 per cent correct responses on the second trials of those problems in which the initial choice was incorrect. Their performances on

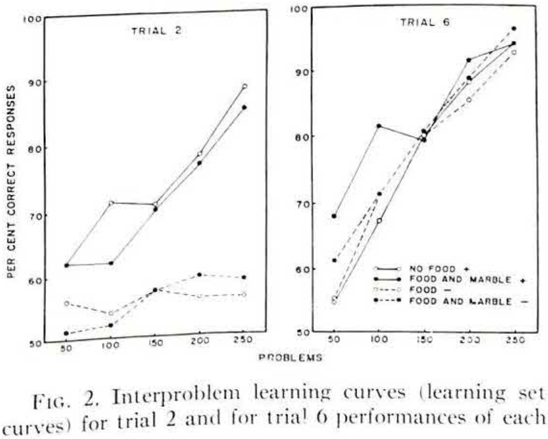

FIG. 2. Interproblem learning curves (learning set curves) for trial 2 and for trial 6 performances of each group.

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[2] Complete summaries of the analyses of variance are available from the author.

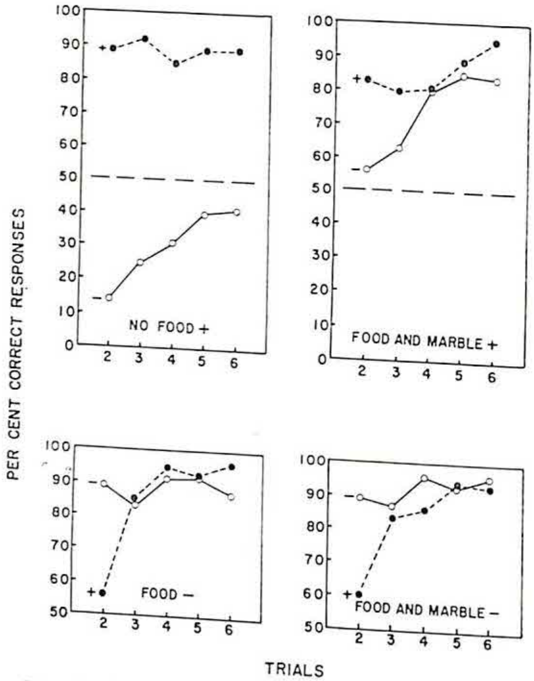

FIG. 3. Comparison of performances on trials 2 through 6 following a correct first trial and following an incorrect first trial. All data are based on a series of 50 problems inserted after completion of the first (differential treatments) phase of the experiment. Panel labels refer to experimental treatments during first phase of the experiment.

these problems never exceeded 40 per cent correct, even for trial 6.

A number of comparisons may be made between this figure and Figure 1. (*a*) Note the (+) curves (Fig. 3) for Groups No Food (+) and Food and Marble (+). They are practically identical to the top curves of Figure 1 for the same groups. (*b*) A similar comparison of the (−) curves of Figure 3 for Group Food (−) and Group Food and Marble (−) shows a marked difference from the equivalent curves shown in Figure 1. Greater agreement can be obtained by comparing the top curves shown in Figure 1 with the (+) curves of Figure 3 for these groups. This agreement exists despite the opposing roles of food on trial 1 in the two situations.

DISCUSSION

The present experiment has extended a previous one (3) by (*a*) reversing the usual role of reward or its absence on trial 1 of a series of problems, and by (*b*) simultaneously pairing a presumably neutral object with a rewarding one. Direct information concerning *a* above may be obtained from the comparison of the results for Group Food (−) and Group No Food (+). For both groups trial 1 presents erroneous information. For the Food (−) group, performance on trial 2 stays close to a chance level, but for Group No Food (+) it rises to nearly 90 per cent correct. Thus, the effects of the misleading information obtained by Group Food (−) on trial 1 carry over to the next two or three trials, but the misinformation obtained by Group No Food (+) is ignored on trial 2. This result obtains even though the two conditions are similar in that the interpretation of the consequence of an initial response is reversed on trials 2 through 6.

The simultaneous presentation of both food and marble on trial 1 seems to add nothing essentially new to the intraproblem learning curves. The successive intraproblem learning curves for Group Food and Marble (+) are very similar to the curves for the Food (+) and the Marble (+) groups of the previous experiment. Whatever difference may exist probably lies in the relatively low initial performance (first 50 problems) of the Food and Marble (+) group. A similar comparison among the curves for Group Food and Marble (−), Food (−), and Marble (−) of the previous experiment shows these three treatments to be essentially equivalent in effect.

A comparison of the results of Group Food (+) with Group Food (−) reveals marked differences in performances. Differences in performance between Group No Food (+) with No Food (−) are negligible. These comparisons, like others cited earlier, are interexperimental in nature.

The data for Phase II reveal that the effects of the differential treatments carried over from Phase I. Groups trained to perseverate a preference in Phase I ([+] groups) did so in Phase II; those trained to suppress an initial preference transferred this response to Phase II. The two (+) groups had their greatest difficulty with problems in which the initial choice was wrong, whereas the two groups trained to suppress the initial preference ([−] groups) made more errors on trial 2 if trial 1 was correct.

SUMMARY

Four groups of naive rhesus monkeys were tested on a series of six-trial object-quality discrimination problems. All animals were treated alike on trials 2 through 6 of each problem. The groups differed, however, in terms of the procedures prevailing on the first trial of each problem. One group received no food on its first choice, but received food reward for repeating the selection on the remaining five trials. A second group found food and a marble on trial 1 of each problem, and the members of this group had to repeat the initial selection to obtain food reward. A third group found food and a marble under the object chosen on trial 1 but had to select the other object on trials 2 through 6. A fourth group found food on trial 1 but had to select the other object on the subsequent trials. The noncorrection procedure was used. The results showed that the two groups trained to perseverate their initial choices eventually attained a high percentage of correct responses on the second trials of the problems. Those groups which had to reverse a response continued to have difficulty throughout the experiment. Group differences in respect to response to correct and incorrect initial choices were maintained in a series of 50 additional object-quality discriminations, even though all groups were treated alike.

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A SEQUENTIAL CUE AND FIXATION IN THE RAT

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Analysis of the jumping patterns present in previous fixation experiments using the Lashley jumping apparatus (2, 3, 4, 5) reveals the possibility that the rat may learn to use a temporal or sequential cue during the insoluble problem. Furthermore, this cue should continue to be effective in the soluble problem. In the soluble problem, for instance, it is customary to have four standard patterns of 10 trials each, which are repeated over a period of 200 trials. In the first pattern, after a fall to the net, the probability of entry and reward on the succeeding jump is three times the probability of a fall to the net. On the following two patterns, the probability of entry following a fall is three to two; and on the fourth, the probabilities are even (two to two). The 3:1 ratio is illustrated in Table 1. If an expectancy of reward following a fall to the net were to develop on the basis of the aftereffect of the fall as a cue, it would be randomly reinforced at a ratio of 11 reinforcements to 7 nonreinforcements; the animal would fall once or twice, but no more than three times consecutively, with the next jump being followed by entry and food reward.

An experiment was designed to test the possibility that such an expectancy[1] is learned. If such be the case, the implication is that fixation may, at least, in part be explained by this particular habit formation.

METHOD

Subjects

The *Ss* were ten albino rats, five male and five female, approximately 150 days old at the beginning of the experiment. They were from the colony of the Psychology department of Michigan State College, and had not been previously used for experimental purposes.

Procedure

A standard Lashley jumping stand (4) was used. The curved shield directly above the windows, which prevented jumping over the apparatus, was black, and the remainder of the apparatus was natural plywood. The rats were placed on a reduced daily diet of 9 gm. of Purina checkers and given all training under a mean of 19 hr. of food privation. During four days of habituation *S* was handled and placed on the jumping stand, which was located directly against the two open windows. The *S* stepped easily to the food platform and consumed its daily food ration before being removed. Next, *S* was required to learn to jump to the food platform from a progressively greater distance, care being taken to distribute the jumps to both windows so that a position habit would not develop during this phase of training. Two alternated cards covered one-third of each window. The cards were those used by Maier (4), a white circle on a black background and a black circle on white.

When all rats had learned to jump a distance of 8 in. to the food platform, the windows were gradually covered by the cards, and the rats learned to knock them down to gain access to the food. Next, each *S* was conditioned to make the required jump to the tap of a pencil. This was accomplished by tapping alternately on the stand and on the rat's tail during 40 trials of 100 per cent reward. This procedure reduced the amount of noxious goading required to elicit the jumping response during and after the insoluble problem.

The *S* was then given 80 trials in the insoluble problem, during which time both windows were randomly locked 50 per cent of the time. No more than 5 of the 10 daily trials could lead to entry, and thus no card was reinforced more than 50 per cent of the time. The mean number of entries following falls to the net compared with the mean number of falls following falls was 12 to 5, distributed in the following fashion: On days 1 to 8 the ratios of entry to fall following a fall to the net were 4:0, 3:1, 3:1, 3:2, 3:2, 2:2, 2:2, 4:0, respectively. This schedule permitted a comparison of performance at the beginning and at the end of the insoluble problem in terms of latencies on 4 trials on each of two days. Latency of response was measured from the time an animal was placed on the stand until a jump was made. Other pertinent aspects of *Ss'* behavior were also consistently recorded.

After falling into the net, *S* was allowed to remain there for 30 sec. while *E* changed or simulated a change of cards. Upon gaining access to the food, *S* was allowed to eat for 30 sec. while *E* changed or simulated a change of cards, before being replaced on the jumping stand. Failure by *S* to jump within 60 sec. after being placed on the stand was followed by 30 sec. of tapping on the stand. After 90 sec. on the stand, *S* was tapped on the tail with a pencil until a jump was made.

All *Ss* were given the soluble problem the day following the last day on the insoluble problem with the above procedure prevailing, except that for half the animals a jump to the white circle was consistently reinforced and for the other half the black circle was posi-

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[1] Conversely, it is quite possible that a negative expectancy or an avoidance response may be conditioned to the aftereffect of eating on the food platform. But, for the most part, the data were so analyzed as to consider the two possible habits as one.

TABLE 1

Patterns of Jumping Which Yield a 3:1 Ratio of Entries to Falls After a Fall to the Net

Trial	Insoluble Problem			Soluble Problem		
	Card Position		Consequence of Jump	Card Position		Consequence of Jump
1	W	B	Fall	B	W	Fall
2	B	W	Entry	W	B	Entry
3	W	B	Fall	W	B	Entry
4	B	W	Fall	B	W	Fall
5	W	B	Entry	W	B	Entry
6	W	B	Entry	W	B	Entry
7	B	W	Fall	B	W	Fall
8	W	B	Entry	W	B	Entry
9	B	W	Entry	B	W	Fall
10	B	W	Fall	B	W	Fall

Note.—*W* is white circle; *B* is black circle. In the insoluble problem, *Fall* means both windows were locked and *Entry* means both windows were unlocked. In the soluble problem, the pattern is for a rat fixated to the right for which *B* is positive, or for a rat fixated to the left for which *W* is positive.

tive and the white circle negative. The soluble problem contained four standard patterns, yielding an 11:7 ratio, which were rotated throughout the 200 trials of the soluble problem. A typical pattern and the way it functions during the card discrimination are illustrated in the right half of Table 1.

RESULTS

All animals continued to eat throughout the experiment, and all ten rats developed position stereotypes during the insoluble problem. Two rats learned the discrimination, one after 40 trials, the other after 70. One rat remained variable throughout the soluble problem. Seven rats reached the fixation criterion of 200 trials with the same incorrect response.[2]

The median latency for the jumps following fall-to-net and the median latency for the jumps following entry-to-food-platform were computed for the first ten trials and the last ten trials of the insoluble problem for each *S*. The difference between these measures (the latter minus the former) was determined for each set of ten trials. On the first ten trials the mean difference ($M = -22.5$ sec.) indicates a longer latency following fall-to-net. On the last ten the difference is reversed ($M = +2.25$ sec.). Nine of ten *S*s now had shorter latencies for jumps following fall-to-net than on the first ten trials; and six *S*s responded faster following fall-to-net than entry-to-food-platform whereas only one *S* (the one *not* included in the nine above) had done so on the first ten trials. The distributions of these mean differences were quite symmetrical and approximated a normal curve; hence a *t* test for related measures was employed to evaluate the difference between the mean differences ($t = 3.53$, $p = .01$). Thus it seems reasonable to infer that learning to the suggested cue took place during the insoluble problem.

That such learning affected the behavior of the animals during the soluble problem is indicated by the latencies of the eight nonlearning rats when confronted with either the negative card or the positive card on the preferred side on two or more successive trials: Throughout the soluble problem these animals showed less delay in jumping after a fall to the net than after entry and eating. In these comparisons the mean latency, over the entire period of 200 trials, for the response in question was the measure employed, since no unusually long latencies occurred and only an occasional one beyond 90 sec. (the point of administering punishment). The distributions of these mean latencies were not noticeably skewed, and the *t* test was considered to be an appropriate statistic. The mean latency of the first jump in a succession of jumps to the negative card was 48.6 sec.; the mean latency of the immediately following jump was 34.2 sec. This difference yields a *t* of 7.96 ($p = .001$). When these *S*s were confronted with the positive card, the mean latency of the jumps following eating on the platform was 28.1 sec.; the mean after falling was 19.7 sec. This difference is also significant at the .001 level ($t = 7.21$).

DISCUSSION

The data are clear in indicating the operation of the posited sequential or aftereffect cue. As a consequence it seems reasonable to expect that many animals would continue to make the same response during the soluble problem as during the insoluble problem. The response in question is approaching the food platform, but during the insoluble problem this has been mediated by a particular positional response which has been reinforced more consistently to the cue of falling into the net and nonreinforced more consistently to the cue of entry and eating than to any other cue stimuli. Furthermore, during the soluble problem a jump to the cue of having fallen into the net continues to be reinforced almost as often as a jump to the positive card cue because, as long as the rat has a position preference, the sequential cue is reinforced approximately three times a day and the positive card is reinforced only five times a day. It is no wonder that a rat which has learned approach and avoidance responses to the cues of fall and entry remains fixated. For many trials, the responses to these cues should have a greater reaction potential than any other stimulus-response tendency in the situation. The present interpretation is in agreement with the finding of Maier and Feldman (6) that fixated responses are more frequent and stronger when rats are exposed to 160 trials in the insoluble problem than when exposed to 80.

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[2] At the end of the experiment, five of the animals which became fixated were given a "fixation breaking" session which consisted of gradually moving the jumping stand to the right for right-fixated animals until the rat jumped against the wall, then back to the median position, then out to the right, and finally back to the median position. Animals fixated to the left were moved to the left. Both windows were wide open during this session. For those interested, this generalization technique, together with the results, is available in a series of photographs in the original report (1).

SUMMARY

Because of the jumping patterns in fixation experiments it is possible that a fall to the net may serve as an important cue which will continue to be effective in the ensuing soluble problem, serving to interfere with the learning of a card discrimination. A typical fixation study, using ten rats on a Lashley jumping stand, was conducted to test the hypothesis that this sequential cue was operative.

The results indicate that learning took place to the cue and influenced behavior during the soluble problem. The eight animals which did not learn the discrimination jumped more quickly on the trial following a fall to the net than on a trial following entry and reward, regardless of whether a positive or negative card was on the preferred side.

The results were interpreted as contributing to an explanation of fixation in the rat.

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DISCRIMINATION ALONG A SIZE CONTINUUM FOLLOWING ABLATION OF THE INFERIOR TEMPORAL CONVEXITY IN MONKEYS[1]

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Several recent studies (reviewed in 3) have demonstrated marked impairment of visual discrimination in monkeys with temporal lobe lesions. This evidence presents difficulties for theory which accords an exclusive role in vision to the geniculo-striate system. One suggestion, made tenable by the absence of visual field defects in temporal operates, has been that damage to the temporal lobes interferes with an essential nonvisual function, termed a "comparison attitude" or "comprehension of the total training situation" (2), rather than with visual processes directly. In support of this hypothesis Lashley (2) has cited data, gathered by Chow (1), which demonstrate that monkeys trained postoperatively on new visual discriminations show recovery of other discriminations acquired prior to operation; without such training, reacquisition of the preoperative discriminations is retarded. Since the additional experience was provided on *new* tasks, the rapid recovery on the original tasks suggested transfer of a reacquired set—"perception" of the discriminanda, or "memory" for the rewarded stimulus, having been unaffected by the surgery.

Other evidence, however, opposes such an interpretation. Riopelle and Ades (7), and the senior author (4), have shown that temporal operates may learn or relearn an easy visual discrimination as quickly as controls, thereby demonstrating successful adaptation to the experimental procedure, yet subsequently show marked deficit in the learning or retention of a more difficult visual problem. These results were obtained in studies which employed a series of qualitatively different visual discriminations (of objects, hue, brightness, and pattern), and it might be argued that the training which the operates received in discriminating stimuli differing in a particular dimension did not provide the appropriate set for the discrimination of stimuli differing in another, perhaps more complex, dimension. The present experiment attempted to avoid this difficulty by providing preliminary training on a discrimination qualitatively *similar* to the test discriminations, the stimuli for all these tasks differing only along the dimension of size. Under such conditions, training to criterion on the first stimulus pair should, presumably, insure both adequate "comprehension" of the situation and the proper "comparison attitude" for discrimination of the other stimulus pairs in the series.

In an attempt to verify results obtained previously on transfer between qualitatively *different* discriminations, the animals were presented with a visual pattern discrimination after they had received the discriminations along the size continuum.

METHODS

Subjects

Six immature rhesus macaques, naive with respect to discrimination training, served as *S*s for the entire experiment. An additional group of 15 naive rhesus macaques was trained on the visual pattern discrimination only.

Apparatus

The apparatus has been described previously (5). It consisted essentially of an enclosure for the animal cage; a testing tray with two food wells, each 1¼ in. in diameter, spaced 18 in. apart; a vertical sliding panel which concealed the baiting of the food wells; and a one-way–vision screen which concealed *E*.

Size Discrimination

Initial training. Two animals with ablations of the inferior convexity of the temporal lobes (IT-55 and IT-58, "post-post" group) and four nonoperate controls (N-39, -56, -57, and -63) were trained to discriminate between discs 3 in. and 6 in. in diameter. (IT-55 and IT-58 were started on the problem 35 and 10 days after operation, respectively.) The incentive was a peanut concealed beneath the smaller disc. The

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two discs, cut from Beaverboard and painted flat black, were placed in random sequence over the two food wells. Thirty trials a day were presented until the animal attained a run of 25 consecutive successes.

First run. The 3-in. disc (consistently rewarded) was then paired successively with a 5-, 4-, $3\frac{1}{2}$-, $3\frac{1}{4}$-, $3\frac{1}{8}$-, $3\frac{1}{16}$-in., and finally another 3-in. disc (consistently unrewarded), a single pairing being presented on two successive days for 25 trials a day. This procedure, beginning with the 3-in. vs. 5-in. discrimination, was then repeated so that each animal received a total of 100 trials on each of the seven pairings over a period of 28 days of testing. In order to prevent response to irrelevant aspects of the stimulus plaques, several discs of each size were prepared and frequently repainted so that no animal received the identical disc a second day.

Retraining and second run. The inferior convexity of the temporal lobes was ablated in two of the original controls (now IT-57 and IT-63, "pre-post" group), and after a ten-day recovery interval all six animals were retrained in a manner duplicating the initial-training and first-run procedures.

Pattern Discrimination

Following the second run on size discrimination all 6 animals were trained to discriminate a plus sign from an outline square. The discriminanda, each with an area of 3 sq. in., were painted yellow on 3-in. by 4-in. gray plaques. The animals received 30 trials a day on this task until they achieved a criterion score of 90 correct in 100 consecutive trials. Fifteen unoperated monkeys that had not had any previous discrimination training were presented with the same pattern discrimination. A comparison between the learning scores of these 15 naive animals and the scores of the 6 sophisticated animals permitted an evaluation of the effects of intensive size-discrimination training, with and without operation, on the formation of a qualitatively different discrimination.

Anatomy

General surgical and anatomical procedures were the same as those described previously (4), with the exception that the bilateral removals were performed in one stage instead of two. The lesions, shown in the

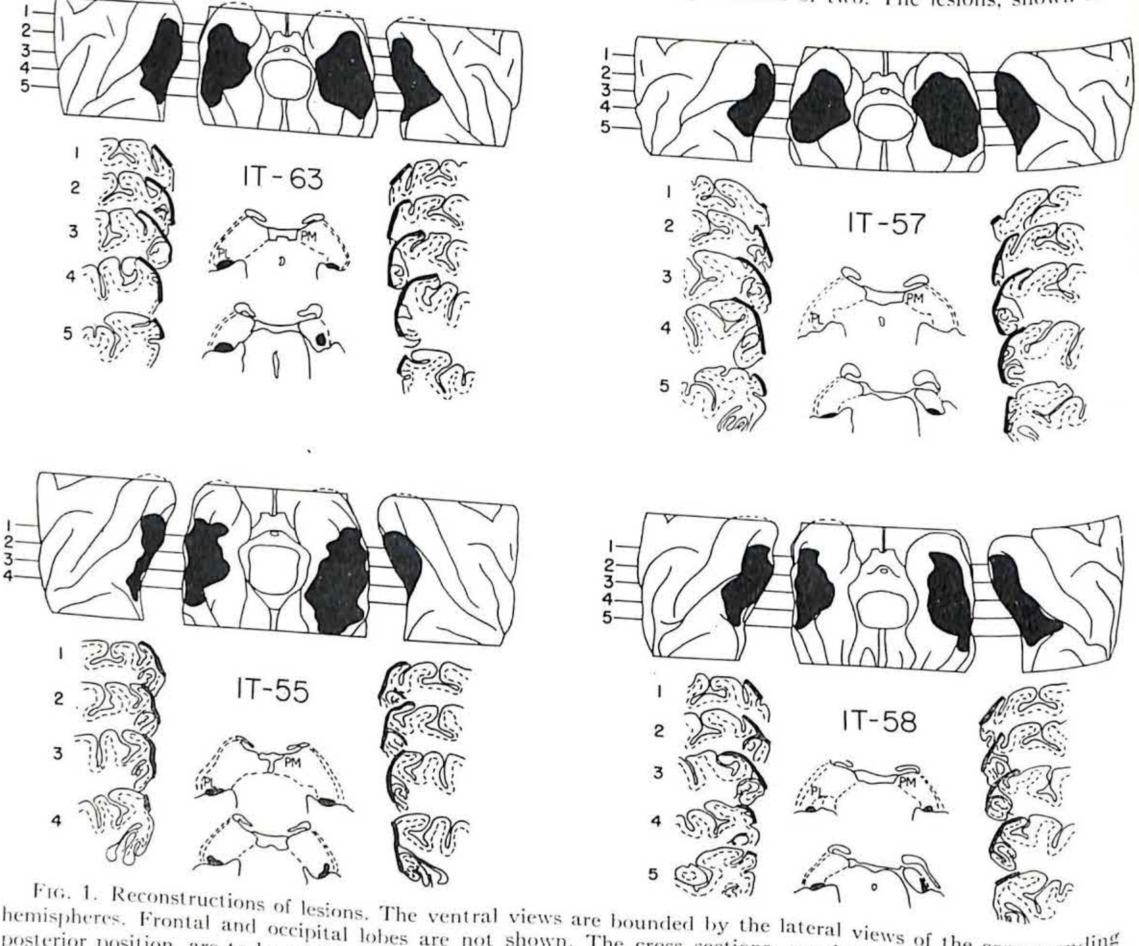

FIG. 1. Reconstructions of lesions. The ventral views are bounded by the lateral views of the corresponding hemispheres. Frontal and occipital lobes are not shown. The cross sections, numbered according to anterior-posterior position, are to be read from top to bottom, in reference to the lateral surface reconstructions placed directly above. The cross sections through the posterior thalamus are labeled *PL* for *pulvinaris lateralis* and *PM* or *pulvinaris medialis*. Black in the reconstructions and cross sections indicates damage; in the thalamus, degeneration.

reconstructions of Figure 1, are similar in locus and extent to those reported in the earlier study. To describe this locus, however, the term "inferior temporal convexity" is used in preference to the earlier designation "ventral surface," since both lateral *and* ventral views are necessary for a complete representation of the lesion. It can be seen from the reconstructions and cross sections that the pole, the banks of the superior temporal sulcus, and the hippocampal formation remained intact.

Retrograde thalamic degeneration is minimal and limited to the ventral portion of the posterior sections of the pulvinar. There is no evidence of degeneration in the laterai geniculate bodies.

RESULTS

Size Discrimination

Scores for initial learning of the 3-in. vs. 6-in. comparison are given in Table 1. Although the post-post operates made approximately twice as many errors as the controls, all the animals attained criterion rapidly. A comparison of these scores with the mean score of the 15 naive nonoperates on the plus-square discrimination (see Table 1) indicates that the discrimination of a 3-in. from a 6-in. disc is a relatively easy task. This conclusion is confirmed by the finding of perfect retention on this problem for the pre-post operates (as well as the post-post operates and nonoperates) after the ten-day recovery interval.

TABLE 1
Learning Scores on Size and Pattern Discriminations for All Groups

Group	Size Discrimination				Pattern Discrimination	
	Initial Training		Retraining		Initial Training	
	Trials	Errors	Trials	Errors	Trials	Errors
Nonoperates (pre-pre)						
N-56	78	20	0	0	150	68
N-39	89	28	0	0	120	61
Operates (pre-post)						
IT-63	58	23	0	0	520	210
IT-57	74	27	0	0	680	258
Operates (post-post)						
IT-55	107	46	0	0	220	92
IT-58	211	66	0	0	470	204
Naive nonoperates ($N = 15$)						
Mean					260	119
Range					130–510	51–245

Note.—Scores are trials and errors *preceding* criterion. For the 3-in. vs. 6-in. size discrimination the criterion was 25 correct in 25 consecutive trials; for the plus vs. square painted-pattern discrimination it was 90 correct in 100 consecutive trials.

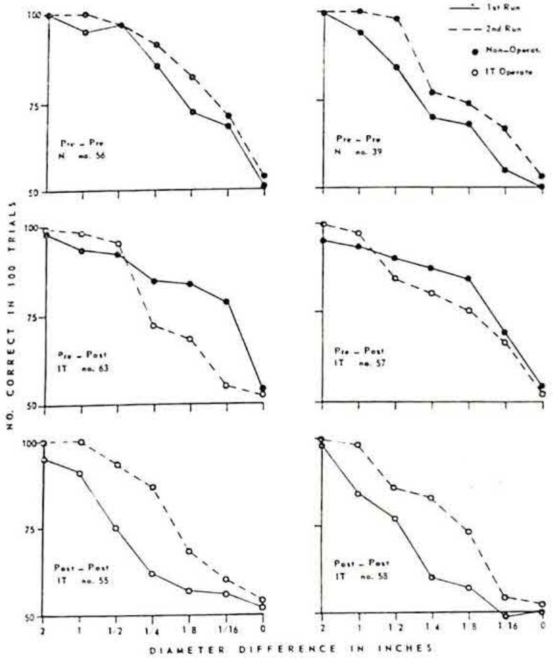

FIG. 2. Scores for each of six animals on first and second runs of size discrimination. The discrimination level *2* denotes the 3-in. vs. 5-in. pairing; *1*, the 3-in. vs. 4-in. pairing; etc.

Performance curves for each of the six animals on both the first and second runs are shown in Figure 2. It may be noted that the successive differences between the 3-in. disc and the others form a geometric progression; for convenience, the six levels of discrimination are plotted as equidistant, with the 3-in. vs. 3-in. pairings (designated as "0" difference in the figure) included for comparison. Performance on 3 in. vs. 3 in. was close to chance, suggesting that the experimental conditions were adequately controlled.

Figure 3 compares the first-run performance of each of the two post-post operates with that of the four controls. Both groups achieved nearly 100 per cent accuracy on 3 in. vs. 5 in., gradually diverged to a maximum separation at 3 in. vs. 3¼ in., and converged again to chance scores at 3 in. vs. 3 in. The inverse sine transformation was applied to the scores for each of the six discrimination levels, and these transformed data were entered in an analysis of variance. The results indicate that the difference between the operate and control groups ($F = 3.78$ with 1 and 4 df) and the differences

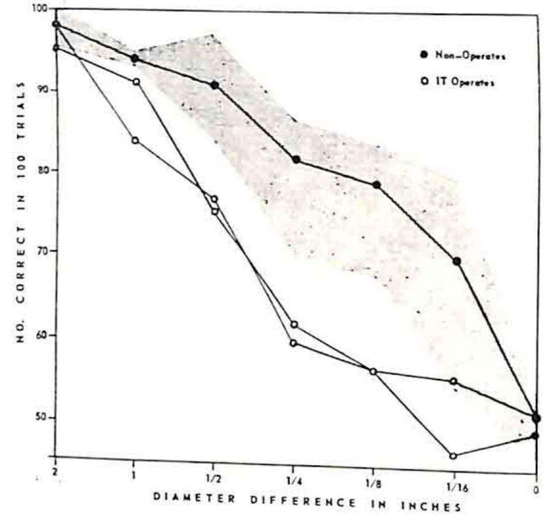

FIG. 3. Scores for two operates and four controls on the first run of size discrimination. Shaded area indicates the range of performance of the four nonoperate controls.

among the six discriminations ($F = 37.60$ with 5 and 20 *df*) are significant beyond the .01 level. The group-by-level interaction does not attain significance ($F = .78$ with 5 and 20 *df*), suggesting that the operates performed more poorly than controls throughout the range of discriminations studied. It should be noted that a significant interaction in the raw scores may have been eliminated as a result of the transformation.

Changes in performance from the first to the second run for the three groups—nonoperate controls, pre-post operates, and post-post operates—may be determined from an inspection of Figure 2. Whereas all groups showed gains in discriminating large differences, only the controls and post-post operates continued to improve as the difficulty of the discrimination increased; the pre-post operates, in contrast, showed a decrement in performance at the more difficult levels. An analysis of variance was performed on the differences between the transformed first-run and second-run scores, for each of the last five discrimination levels. (Inclusion of the first level—3 in. vs. 5 in.—would have biased the scores of the nonoperates in the direction of no change, since both animals attained 100 per cent correct on both runs.) The results of the analysis of variance indicate that the difference among the groups is significant beyond the .05 level ($F = 24.87$ with 2 and 3 *df*); *t* tests run for individual comparisons show that the difference between the post-post operate and control groups is not reliable, but that both groups differ reliably from the pre-post operates ($t = 3.00$ and 2.35, respectively, 3 *df*, one-tailed test; $p = .05$). The other comparison which attains significance is that among the discrimination levels ($F = 4.70$ with 8 and 12 *df*; $p = .05$), indicating that changes in performance varied with the difficulty of the tasks. The absence of significant interaction between groups and levels ($F = .96$ with 8 and 12 *df*), despite a suggestion of such interaction in the raw scores (see Fig. 2), may again be the result of the transformation.

Pattern Discrimination

Trial and error scores of the six animals on the plus-square pattern discrimination are presented in Table 1. It may be noted that there is no overlap among the scores for the three groups, the nonoperates learning most quickly, the post-post operates next, and the pre-post operates last. Comparisons between the performance of each of these groups and the performance of the 15 naive, unoperated animals show that the nonoperates fall at the lower extreme of the distribution of naive normals, the post-post operates are well within the range, and the pre-post operates are slightly retarded, falling at the upper extreme of the distribution for the naive control group. The probabilities of the nonoperates and pre-post operates obtaining such extreme trial scores by chance are .05 and .01, respectively (two-sample test [6]).

DISCUSSION

Results on the 3-in. vs. 6-in. size discrimination confirm an earlier observation (5) that temporal lobe damage may have no demonstrable effect on retention of an easy visual task, and yet produce impairment in the initial learning of that task. The learning deficit found in the present study was slight, however, and in both initial training and retraining all animals were brought quickly to a level of 100 per cent correct before they were presented with the discrimination continuum. To maximize the opportunity for positive transfer, the difference between the rewarded and unrewarded discs was reduced by a series of small steps. The operates continued to discriminate throughout this series, their performance indicating a gradual, rather than an abrupt, transition from perfect scores to chance. Nevertheless, the performance of the post-post operates on the first run, and of the pre-post operates on the second run (as compared with their performance on the first), fell significantly below the equivalent measures for the nonoperate controls. This finding, which may be expressed as an increased difference limen for visual size, demonstrates that temporal operates may show impairment on a discrimination continuum even after they have been trained to discriminate stimuli differing in the relevant dimension.

The intensive training provided on the size discriminations did appear to facilitate the post-post operates' performance on the pattern discrimination, their learning scores falling well within the range of scores obtained by naive, *unoperated* animals. However, the two nonoperate controls learned significantly more rapidly than the naive animals, maintaining their superiority over the operates. Without the nonoperate controls the results might have led to the erroneous conclusion that training operated animals on one task produced complete recovery in their performance on another.

The implication of these results is not that the temporal operate's performance is permanently impaired (a more extended testing period would be required to clarify this point), but, rather, that a general readaptation to training is insufficient to overcome the deficit.

SUMMARY

The purpose of the study was to determine whether or not impairment in the visual discrimination performance of temporal operates could be overcome by preliminary training with stimuli qualitatively similar to the test stimuli. Two operated and four control monkeys were trained to discriminate a large difference in visual size and were then presented with a graded series in which this difference was gradually reduced. Following this training, two of the original controls were operated and all six animals were retrained on the largest difference before receiving the discrimination continuum a second time. Although the temporal operates rapidly attained the criterion of 100 per cent correct on the initial size discrimination, their scores on the subsequent size discriminations fell significantly below the scores achieved by the nonoperate controls. This impairment may be expressed as an increased difference limen for visual size. The results are interpreted as providing evidence against the view that a loss of a "comparison attitude" or of "comprehension" of the training situation accounts for the impairment in the visual discrimination performance of temporal operates.

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ANTICIPATORY AND PERSEVERATIVE ERRORS FOLLOWING FRONTAL LESIONS IN THE RAT[1]

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The functions of the frontal cortex are not clearly defined. However, evidence has been adduced recently in support of the hypothesis that the integrity of the frontal areas is essential to the inhibition of "anticipatory" errors in a serial learning sequence. For the purpose of the hypothesis, "anticipation" is defined as the making of a response in a sequential pattern of behavior which, although incorrect when made, would be correct later in the sequence. Carpenter (1) suggests that the intact frontal cortex exercises an inhibitory influence upon this type of error and that with loss of, or damage to, the frontal cortex this inhibition is diminished so that anticipatory errors increase. Stellar, Morgan, and Yarosh (9) and Epstein and Morgan (3) have pursued this line of inquiry with the more general hypothesis that the frontal areas mediate some "symbolic processes." The proper functioning of these processes is regarded by them as necessary to the carrying out of a behavior sequence, and interference with them results in failure to make the series of responses in the correct order. Maze-choice and rate-of-running problems have been used to examine these hypotheses.

Certain methodological requirements are implicit in the testing of the hypothesis that anticipatory errors increase following injury to the frontal cortex. It would appear to be mandatory that the problem be designed so that, at those points at which anticipatory errors are predicted, other errors of a non-anticipatory nature are available to the animal. The significance of the anticipatory errors may then be evaluated more legitimately. The importance of this may be inferred from examination of reports already extant on the problem. Carpenter has described the evidence accumulated to date as somewhat contradictory, and contrasts his own results and those of Jacobsen (5) and Crawford (2) with the data obtained by Epstein and Morgan. He suggests that the latter, who used speed of running in a straightway, were not measuring anticipation in the sense in which other investigators have defined it. He interprets his own data and those of Jacobsen and of Crawford as indicating that extirpation of the frontal areas "produces a behavior which can be described as release from frontal inhibition." It can be pointed out, however, that the only errors available to the animals in these studies were, by virtue of the apparatus and experimental design, anticipatory in character. Thus, it is difficult to be sure that these errors represented the loss of some kind of inhibition or whether they were simply erroneous responses. The fact that these errors occurred more frequently at choice points in the middle of the sequence than at the beginning or end may be a reflection of the relatively greater instability of the habit at these points. It might be observed in passing that a possible tendency to make position-preference errors when a counterpreference position habit has been impaired may also operate to cast doubt upon the interpretation of data gathered in this kind of problem.

In this study an attempt has been made to test the anticipation hypothesis within a methodological framework intended to minimize these ambiguities.

METHOD

Subjects

The *S*s were ten naive, male albino rats over 90 days old; two animals failed to survive the operation. They were maintained in the animal quarters of the Neurophysiology Laboratories, Neuropsychiatric Institute of the University of Illinois.

Apparatus

A modification of Fields's SMVDA (4) was used (see Fig. 1). It consisted of an alley, 6 ft. by 4 ft., constructed of 1/4-in. plywood and painted inside with Delta Milwaukee machine-gray enamel. The alley was divided by black, lateral screens into four equal compartments. Into each screen were cut four equally

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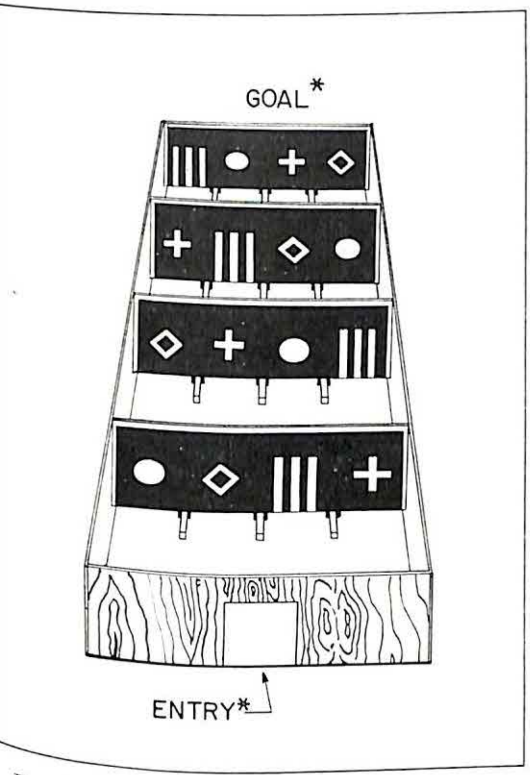

FIG. 1. Main alleyway. Position of entry and goal oxes indicated by labels.

aced apertures 4½ in. square. Each aperture was tted with a trap door upon which was painted a hite symbol. The symbols used were a disc, a cross, hollow diamond, and three vertical stripes. The ap doors were interchangeable so that their positions the screen could be varied at will. A series of brass cking rods and cotter pins was used to secure the ap doors from behind so that any three could be cked while the fourth, resting vertically on its own ase, could be pushed over with gentle pressure, ereby giving access to the next compartment. A arting box under the control of *E* gave admission to e first compartment while the unlocked door in the urth and final screen led into a feeding goal box.

rocedure

The sequence of unlocked doors was arranged so at, in order to reach the goal box, *S* was required to proach and displace the striped door in the first ree screens in succession and the door marked with e disc in the fourth screen. To eliminate any position abit the relative position of the doors in each screen as changed after each trial in accordance with a hedule derived from a table of random numbers. An rorless trial was recorded whenever an *S* passed rough the alley without touching any of the locked ors. Contact with any locked door was scored as an ror. The animals were maintained on a 22-hr. food eprivation schedule and on reaching the goal box ere permitted to eat for 2 min. from a bowl of wet ash consisting of one part Purina Dog Chow to one part water by weight. For the purposes of this experiment the sequence was regarded as learned when *S* succeeded in completing without error nine out of any ten consecutive trials.

Before introduction to the main alley a brief period of pretraining was given in a 36-in. by 8-in. runway in which were two plain black trap doors leading to a goal box. This was intended to facilitate the acquisition of the trap-door-pressing response without affecting the discrimination and sequence aspects of the main apparatus. Twenty-five trials were given in this pretraining period.

As each animal reached criterion in the main alleyway, it was returned to ad libitum feeding for three days and then assigned to either the control or the operative group. Animals were assigned on the basis of the number of trials to reach criterion so that the groups were matched for rate of acquisition. On the fourth day the lesions were performed on operative-group animals, which were then rested for a ten-day recuperative period.

The cortical lesions were made by a technique essentially the same as that described by Richter and Hawkes (7). Under Nembutal anesthesia an incision was made in the mid-line of the scalp. The fascia were removed, the coronal suture was identified, and two holes were drilled bilaterally at a point approximately 3 mm. anterior to it. The meninges were pierced with a sterile needle and the cortical tissue removed by negative pressure through a glass cannula. The cannula was manipulated as far as possible anterior to the drill holes, and care was taken not to remove tissue posterior to the point of entry. Two animals died during operation, apparently because of the inadvertent use of deteriorated Nembutal. For the first five days postoperatively the animals were fed a diet of milk, bread, and ground carrots. During the remaining five days they were returned to the 22-hr. deprivation schedule.

Animals assigned to the control group spent the same period at rest and subject to the same feeding schedule. On the eleventh postoperative day trials were resumed in the main apparatus. These trials, like the original series, were run at the rate of two per day and extended over a period of twelve days. On completion the brains of the operated animals were preserved in formaldehyde. A total of four operated and four control animals remained for inclusion in the final data. Diagrammatic maps of the lesions are given in Figure 2.

RESULTS

The analysis of the results follows the accepted convention, being based on first-choice errors. The anticipatory hypothesis demands that when an operated animal makes an error in the first three screens, this error will be most frequently that of choosing the trap door marked with a disc, this being the correct choice at the fourth screen. Anticipatory errors of this kind are to be expected to increase in frequency at the second and third screens. It is also necessary to show that this error is made

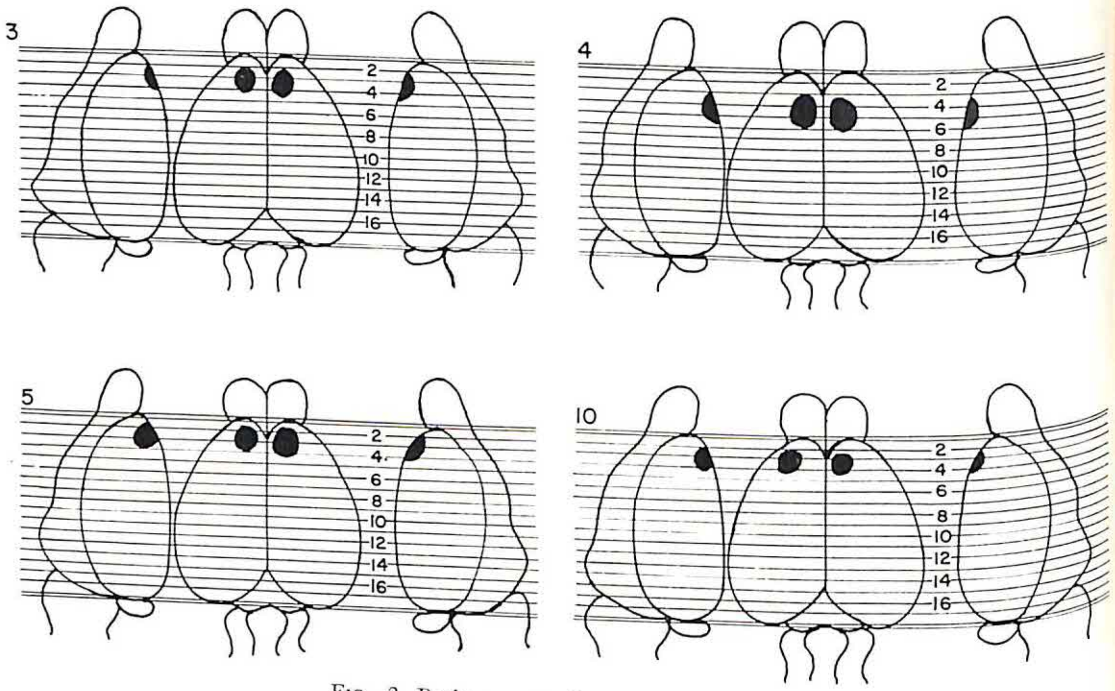

FIG. 2. Brain maps of operated animals.

with significantly greater frequency by the operated animals than the control animals. The distribution of first-choice errors by both groups at each screen is given in Table 1.

The statistical problem here is to decide whether the obtained distribution of first-choice errors between the two groups is random, or whether it varies with presence or absence of cortical injury. With a group of this size, providing data which are not independent, it was felt that nonparametric statistical analysis would be justified. This has been achieved by ranking each *S* according to the frequency of its scores on each variable, and testing the arrangement of the ranks with the Mann-Whitney *U* test (6). Rankings have been made on the basis of (*a*) anticipatory first-choice error scores at each of the first three screens, (*b*) perseverative first-choice error scores at the fourth screen, and (*c*) *total* errors made at each screen. The values of *p* obtained are given in Table 2.

Inspection of both tables shows that no positive conclusions may be drawn regarding the incidence of anticipatory errors. It should be noted that the operative group did produce more anticipatory errors at each of the first three screens than did the control group. The failure of these differences to reach conventional levels of statistical significance cannot be regarded as sufficient evidence to refute the hypothesis under examination. On the contrary, the fact that the differences obtained are in the direction predicted by the hypothesis might be regarded as evidence in its favor.

TABLE 1
First-Choice Errors of Both Groups at Each Screen

Screen	Group	First-Choice Errors			
		Stripes	Disc	Cross	Diamond
1	Oper.		9	18	21
	Cont.		1	1	2
2	Oper.		1	0	0
	Cont.		0	0	0
3	Oper.		14	0	0
	Cont.		8	0	2
4	Oper.	49		6	9
	Cont.	12		0	1

TABLE 2
Values of *U* and *p* for Rankings Based on Anticipatory and Perseverative Errors

Screen	Errors	*U*	*p*
1	Antic.	2.5	$> .057 < .100$
	Nonant.	0	.014
2	Antic.	6	.343
	Nonant.	8	.557
3	Antic.	4	.171
	Nonant.	6	.343
4	Persev.	0	.014
	Nonper.	4	.171

At the fourth screen differences at an acceptable level of significance are found with respect to perseverative errors. By "perseverative" errors is meant errors of choice which would have been correct at earlier points in the sequence. Operationally, the choice of the striped door at the fourth screen is the only perseverative error which can be made with this apparatus. As similarly significant differences do not exist with respect to other errors at the fourth screen, it seems safe to infer that the perseverative errors are attributable to the effects of the lesions.

DISCUSSION

The inferences which may be drawn from these data are twofold. In the first place they are insufficient to refute the hypothesis that lesions of the frontal cortex are followed by anticipatory errors in a serial-discrimination task. If the simple number of such errors made by both groups is taken into account, the data point instead toward a trend in favor of the hypothesis. However, the lack of statistical significance in these differences compels the conclusion that the findings of previous studies are not substantially challenged.

A second inference relates to the phenomenon of perseveration. Perseverative errors seem to be clearly related to the effects of the lesions. As an aid to interpretation it might be of value to provide a nonquantitative account of the postoperative behavior of the operative rats. Quite typically the animal, when first placed in the starting box and then admitted to the first compartment, displayed rapid and varied approaches to the trap doors. It tended to scurry from one to another, sometimes pushing and sometimes not, and often touching the trap door so gently that it failed to fall. When the correct trap door was finally opened, the rat usually ran into the next compartment without delay and went straight to the correct trap door. The correct response was continued to the fourth screen, where its incidence is reflected in the high total of perseverative errors already reported. The contrast between the apparent "randomness" of the animals' behavior at the first screen and their highly directive behavior at the subsequent screens was most striking to the observer.

It is possible that this behavior might be akin to that reported by Settlage, Zable, and Harlow (8). They interpret the problem-solving behavior of prefrontal monkeys to indicate that "... the phenomena of perseverative interference will be encountered when successful adaptation requires that a pre-established set be suppressed or modified." The present data may perhaps support the same type of interpretation. However, at the present time they can do no more than suggest bases for speculation and problems for further study.

SUMMARY

1. The distribution of anticipatory, nonanticipatory, and perseverative errors in a serial multiple visual discrimination problem was investigated in rats following lesions to the frontal cortex.

2. No significant differences were found in the incidence of anticipatory errors between operative and control groups.

3. Significant differences were found in (*a*) the occurrence of perseverative errors and (*b*) total postoperative errors made. In both cases the operative group demonstrated the higher frequency of errors.

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TACTILE SIZE JUDGMENT AFTER PENETRATING INJURY TO THE BRAIN[1]

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Studies concerned with the role of the sensory cortex in tactile size judgments are exceedingly rare, and the results paradoxical. Blum, Chow, and Pribram (2) reported no permanent deficit in tactual size discrimination in six macaques after parietal lobectomy in one animal, temporal lobectomy in another, and parieto-temporo-preoccipital ablation in the remaining four. There was, however, severe impairment of other tactual functions in the same animals since four of the six were completely unable to relearn roughness discrimination and three lost the ability to discriminate weights.

Reports for man are somewhat different. Evans' (4) findings in four patients with limited cortical ablation and "marked loss of [sensory] function" show a greater impairment for size judgment. Whereas "weight sense" was "normal" in one patient and recognition of form, shape, and texture preserved in another, recognition of size was affected in all. Head, on the other hand, studying 16 patients with cortical lesions, states that abilities to discriminate size and weight are lost together (5, p. 757), and whenever sensation is affected, appreciation of size is lost (5, p. 589).

These conflicting reports are based upon studies performed on two species and employing three different tests of size discrimination, i.e., "test tubes" (4), "circles" (2), and "circular pieces of leather" (5). Moreover, none of these studies made systematic use of bilateral testing, a technique which has been shown to be particularly capable of revealing sensory deficits (1, 3, 6, 7, 8, 9).

Using bilateral (successive and simultaneous) stimulation, the present writer has demonstrated (9) that brain injury causes a constant error between the supported hands for judgments of weight, and that the direction of this constant error depends upon the somatosensory status of the patient. That is, in a brain-injured group without somatosensory deficit, weights on the hands contralateral to the brain lesion were perceived as lighter than those on the homolateral hand; by contrast, men with brain injury and somatosensory deficit perceived weights on the affected hand as heavier than those on the normal hand. Thus, while *presence* of deficit in weight discrimination was unrelated to presence or absence of tactile deficit otherwise determined, the *direction* of error in weight judgment was significantly related to the sensory status.

The purpose of the present experiment was to determine the relation of tactile deficit to size discrimination and to compare the results with previous data on size and weight judgment.

METHOD

The *S*s, apparatus, and procedure were identical with those of an earlier study of weight discrimination (9) and are briefly described below.

Subjects

Four groups comprising 15 *S*s each were employed: one group with brain injury and evidence of somatosensory impairment of the hand (brain-injured sensory group); the second with brain injury, but without evidence of somatosensory impairment of the hand (brain-injured nonsensory group); the third, with injury to peripheral nerves supplying the hand (arm-injury group); the fourth, with injury to peripheral nerves of the leg (control group).

Apparatus

The stimulus objects employed in this study were two identical solid, circular bronze cylinders. The weight of each was 103.6 gm.; the bases were 31.5 mm. in diameter. The stimulus objects were suspended above the supinated palms of *S*, and were hidden from view. The presentation of stimuli was controlled by a bank of four decade electronic timers. These timers, by energizing and de-energizing two solenoids, controlled the order, duration, and interval between the placement of the stimulus objects upon *S*'s palms.

By means of three switches, the timers could be regulated so that: (*a*) the right palm was stimulated first, and the left, second; (*b*) vice versa; or (*c*) both palms were stimulated simultaneously. In the two successive conditions *S* was required to state whether the comparison (second) stimulus object was larger or smaller than the standard (first). In the simultaneous condition he was required to state whether the stimulus object on the affected hand was larger or smaller than the one on the normal hand.

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Throughout the experiment a pair of objects of only one size and weight was employed, and the duration of contact of the stimulus with the palm was kept constant at 1 sec. At no time was *S* informed of the physical identity of the stimuli.

Experimental Design

The experiment consisted of extensity (size) judgments between two identical stimuli.

In the successive conditions, five time intervals were interpolated between the standard and comparison stimuli. They were: 0.1, 1, 2, 3, and 5 sec. All five intervals were used in each of the two successive conditions, and each was repeated five times, making a total of 50 judgments in the two successive conditions. An *S*'s score for the successive conditions thus was the number of times in 50 trials that the stimulus object on the affected hand was judged to be larger than that on the normal hand. His score for the simultaneous condition was the number of times in ten judgments that the stimulus object on the affected hand was judged larger than that on the normal hand.

RESULTS

The principal effects investigated in this experiment were those of: (*a*) *Locus of lesion*, i.e., a division of the group according to the lobe of the brain injured (frontal, parietal, temporal, or occipital lobes); the right or left cerebral hemisphere; and the groups with peripheral nerve injury of the arm or peripheral nerve injury of the leg. (*b*) *Symptom*, i.e., a brain-injured group with somatosensory impairment of the hand, a brain-injured group without such impairment, and groups with the above-mentioned peripheral nerve lesions. (*c*) *Condition of stimulation*, i.e., simultaneous or successive presentation of stimuli.

Analysis by Locus of Lesion

When *S*s were grouped by locus of lesion, analysis of results revealed no constant errors between the hands for judgments of size. This was true for all groups, whether successive or simultaneous stimulation was employed.

Analysis by Symptom

For this analysis *S*s were grouped according to their symptoms, rather than presumed locus of brain lesion. Neither the brain-injured nonsensory group, nor the two groups with peripheral injury showed a significant constant error between the hands for size judgment. This lack of constant differences between the hands held true for both the successive and simultaneous conditions of stimulation (Fig. 1).

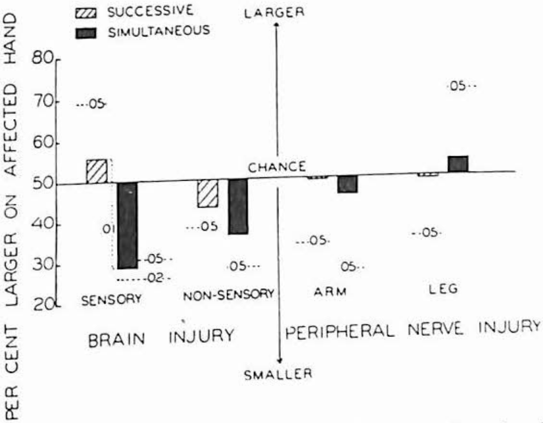

FIG. 1. Constant errors for size judgment. Levels of significance from chance are .05, .02. Means of successive and simultaneous conditions for brain-injured sensory group differ at .01 level.

The brain-injured sensory group, however, significantly underestimated the size of the stimuli applied to the affected hand in the simultaneous condition but did not demonstrate any significant error for the successive condition. The two conditions differed at the .01 level of confidence for this group alone, the simultaneous condition effecting *under*estimation and the successive condition tending to cause *over*estimation. It should be noted, however, that despite the difference in *direction* of the constant errors obtained in the brain-injured sensory group under the two conditions of stimulation (Fig. 1), those *S*s who gave relatively more "large" judgments under one condition tended to give more "large" judgments for the other, the correlation being .46 (falling short of the .05 level of significance).

The correlations between the successive and simultaneous conditions of stimulation were also positive (and significant) for all other groups (.57 for control group, .67 for arm-injury group, .65 for brain-injured nonsensory group).

DISCUSSION

It is of interest to compare the results obtained in the present study of size discrimination with those of a study of the same *S*s for weight discrimination (9), and with those of earlier reports (2, 4, 5). In both of the present author's studies the two peripheral nerve-injured groups showed no constant differences between the hands for size or weight judgment. The brain-injured nonsensory group showed significant underestimation for weight, and the brain-injured sensory group showed overestimation for weight and underestimation for size on the hand opposite the brain injury.

Since all our results were obtained under identical conditions (stimulation of both hands simultaneously or in succession) and in the same *S*s, we can compare the relative impairment of weight and size judgments in our group. Such a comparison shows significantly more errors for weight than for size in our brain-injured *S*s.

While these results obtained on bilateral testing cannot be equated with earlier observations made on unilateral tests, it is clear that the present results parallel those found (on unilateral testing) in subhuman primates (2) and do not parallel earlier findings for man (4, 5). Blum, Chow, and Pribram (2) reported considerable resiliency of size discrimination in monkeys after cortical ablations; the same animals showed more persistent deficit in discrimination of weight and other stimulus attributes. By contrast, Evans' results for man (4) apparently differ from ours, since in his group of cases it was size discrimination that seemed to be most vulnerable to cortical lesions. However, Evans studied a smaller group of cases, did not include controls, and employed only unilateral testing. It would seem that our present result indicating that discrimination of size is less affected than that of weight is more representative of the relative stability of these functions after brain injury.

The greater vulnerability of weight judgments, by our methods, was not apparent from Head's studies, which were based primarily on unilateral testing. Head (5) has stated that when sensation is affected, size judgment is lost. Since in the present study only the brain-injured sensory group showed a defect in size judgment, our results would indicate that neither sensory deficit (as is found in peripheral nerve injury) nor brain injury without such impairment can cause a deficit in tactile size judgment. A combination of both brain injury and sensory deficit proved necessary under these conditions.

Head further reports that appreciation of size and weight are disturbed together. Whereas this association of symptoms held true for the brain-injured sensory group, the brain-injured nonsensory group demonstrated a significant deficit for weight (9) but not for size judgment. In addition, only the brain-injured nonsensory group showed significant positive correlations between size and weight judgments. This again indicates that these functions are not as similar as Head (5) has indicated, at least if tested bilaterally.

Moreover, these functions differ in more ways than their differential resistance to brain injury. Whereas the brain-injured sensory group felt the weight on the affected hand as heavier than that on the normal hand, they also perceived it to be smaller. This relation might at first seem to be best described in terms of the size-weight illusion. However, if the size-weight illusion were operating here, one would rather expect a negative correlation between the perceptual magnitudes of the stimulus object's size and weight. Instead, positive (but nonsignificant) correlations were found between the constant errors of the two modalities for the brain-injured sensory group. The brain-injured nonsensory group also tended to perceive the object on the contralateral hand as smaller, and, contrary to what might be expected from the paradigm of the size-weight illusion, the weights were perceived as lighter by this group.

In conclusion, brain injury affects weight more than size judgment, regardless of the presence or absence of resulting somatosensory symptoms. If the brain injury does not result in somatosensory impairment of the hands, then ability to judge weight is affected alone; if the brain injury results in somatosensory defect, then both weight and size judgment are affected. The latter association of deficits found under those conditions supports Head's (5) conclusion concerning the relation of the abilities to judge size and weight. However, the failure of all but the brain-injured nonsensory group to demonstrate significant correlations between these functions, and the overestimation of weight with underestimation of size in the sensory group implies less similarity of these functions, when tested by these methods, than Head has reported. The greater relative deficit of weight over size discrimination following brain injury is in contradistinction to the findings of Evans (4) but in close agreement with those of Blum, Chow, and Pribram (2). It may be concluded that after brain injury, ability to judge size (with bilateral stimulation) is less frequently affected and less impaired than that of weight, and that the direction and magnitude of the constant error between the hands depends upon both the mode of stimulation and the stimulus attributes.

SUMMARY

1. Constant errors between the supported hands, on estimation of relative tactile size, were determined for four groups of 15 *S*s each. These groups consisted of veterans with: (*a*) traumatic brain injury and consequent somatosensory deficit of the hand, (*b*) traumatic brain injury without such somatosensory deficit, (*c*) peripheral nerve injury of the arm, (*d*) peripheral nerve injury of the leg (controls).

2. Two conditions of stimulation were employed: (*a*) stimuli were applied to both hands simultaneously, and (*b*) the comparison stimulus was applied to one hand following application of the standard to the other hand.

3. Significant constant errors between the hands were found only in the group with brain injury and somatosensory deficit. This error operated to cause relative underestimation of the size of the stimulus on the affected hand, when both hands were simultaneously stimulated.

4. Comparison with results of a previous study of weight judgment on the same population indicates that after brain injury, size is less frequently affected than weight judgment and is less impaired.

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THE RAT'S ADJUSTMENT TO 23-HOUR FOOD-DEPRIVATION CYCLES

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Many experimental designs call for the measurement of performance on consecutive days under conditions of appreciable but uniform motivation. To accomplish this, the *S* is frequently maintained on a daily food-deprivation cycle, with perhaps 60 min. of free ingestion following each day's observation. The animal is then presumed to come to the experimental situation always at the same drive level, designated in this example as 23-hr. hunger.

It is generally accepted that intersession uniformity in motivation is possible only after the animal has been given an opportunity to adjust its feeding and metabolic patterns to the imposed schedule. A critical methodological question immediately arises: How long must the animal be kept on the 23-hr. deprivation cycle before the requisite adjustment is achieved? The answer expressed in practice varies somewhat from experiment to experiment, but with the rat usually falls within the range of 5 to 10 days. Whether or not such a preliminary adjustment period is judged to be sufficiently long to insure the same level of drive on the successive experimental days may depend upon the measure of drive adopted to test the presumption. Body weight, strength or amount of consummatory response, and amount of running in an activity wheel have been variously used as indicators of drive state, but certain observations led us to doubt that these always remain parallel. It seemed desirable, then, to follow several standard measures of drive as they fluctuated during an extended period of rats' subsistence on a 23-hr. deprivation schedule. The data to be presented confirm the suspicion of nonequivalence of the measures, and indicate that, according to at least one index, a 15-day adjustment period is far too brief to bring the animals to a reasonably steady state.

METHOD

In essence the experiment examined the rat's reaction to and recovery from a 35-day period of 23-hr. food-deprivation cycles in terms of food and water intake, body weight, total daily activity in the running wheel, and activity during the hour immediately preceding feeding.

Apparatus. The battery of eight activity wheels, and the methods of environmental control, are described in detail elsewhere (1, 2). The only significant change was the shift of the 12-hr. light phase to the 3:00 A.M. to 3:00 P.M. period.

Subjects. The *S*s were albino rats of pure Wistar strain, approximately 150 days old at the beginning of the experiment. The experimental group and the matched control group were originally assigned eight animals each, but one experimental *S* failed to survive.

Procedure. The experiment was conducted in two sections (5/2/52 to 7/7/52 and 10/20/52 to 12/26/52), with conditions duplicated as closely as possible. Each of these equivalent sections consisted of four successive phases: (*a*) The four experimental and four control rats were first given a 10-day *habituation* period in the activity wheels. Food (Albers Calf Manna) and water were always available, replenished shortly before the daily dark cycle began at 3:00 P.M. (*b*) There followed a 10-day *base-line* period during which the normal activity, ingestion, and body weight were determined for each rat under ad libitum conditions. At 12:40 P.M. on each day the activity of the preceding 23 hr. was recorded from the Veeder counters, and at 1:40 the intervening hour's activity was noted. Between 2:40 and 3:00 the food that remained was weighed to permit calculation of the 24-hr. ingestion; the day's water intake was recorded; the food and water containers were refilled; the animals were weighed; and the necessary cleaning was done. (*c*) The next 35 days constituted the *deprivation* phase. During this time the experimental animals' food dishes were removed each day at 2:40 P.M. and returned on the following day at 1:40 P.M. The schedule of recordings continued unchanged, thus providing daily measures of the running activity during the total 24 hr. and during the hour beginning 22 hr. after last eating; water intake during the day; food intake during the feeding hour; and body weight after eating. The measurement operations for the control rats reproduced those of the base-line period. (*d*) Finally, the rats were returned to the ad libitum base-line conditions for an 11-day *recovery* period.

RESULTS

To emphasize major trends, the 35-day deprivation phase is divided into seven 5-day periods (I–VII), and compared with the last 5 base-line days. Each rat's mean for a given 5 days is first computed, and the median of the several rats' means then determined. Table 1 presents these medians for the seven experimental and the eight control *S*s, for the meas-

TABLE 1

Effect of 23-Hr. Food-Deprivation Cycles over 35 Days
(Medians of individual* means for successive 5-day periods)

Period	Body Weight (gm.)		Food Intake (gm.)		Water Intake (ml.)		Total Daily Activity (revolutions)		Prefeeding-Hour Activity (revolutions)	
	Exper.	Control	Exper.	Control	Exper.	Control	Exper.	Control	Exper.	Control
Base	310	325	18.2	18.2	32.4	36.3	493	521	0	0.0
I	282	333	6.8	18.6	20.9	31.6	1457	521	60	0.0
II	252	333	8.5	18.0	18.1	35.1	3242	525	123	0.2
III	229	333	9.0	18.8	21.6	34.9	5297	430	262	0.0
IV	223	334	11.0	19.9	19.8	34.7	4130	357	305	0.0
V	229	336	11.9	20.1	29.6	37.1	4733	385	972	0.1
VI	223	340	11.2	18.9	26.4	36.3	5752	325	1077	0.2
VII	214	341	11.4	19.8	26.8	31.6	6664	370	1671	0.2

* Experimental $N = 7$, control $N = 8$.

TABLE 2

Recovery Following 35 Daily 23-Hr. Food-Deprivation Cycles

(Medians)

Condition	Body Weight (gm.)	Food Intake (gm.)	Water Intake (ml.)	Total Daily Activity (revolutions)	1-Hr. Activity (revolutions)
Control	338	19.3	35.9	348	0
Exp. base	310	18.2	32.4	493	0
Exp. recovery day					
1	228	18.0	48.0	192	16
2	235	21.0	40.0	933	39
3	242	20.0	37.0	910	78
4	248	22.5	43.0	1074	8
5	253	24.0	46.0	792	3
6	253	22.0	46.0	364	11
7	258	22.0	46.5	460	0
8	262	22.0	42.0	327	0
9	265	21.0	39.0	358	0
10	267	20.0	39.0	555	0
11	271	20.0	38.0	393	1

ures of body weight, food intake, water intake, total 24-hr. activity, and activity during the hour immediately preceding feeding ("prefeeding-hour activity"). It is clear that the two groups, closely similar during the base-line period, differ sharply in all measures during the seven periods of differential treatment, and that at least the 1-hr. prefeeding activity of the experimental rats is still increasing at the end of the 35 days. In Table 2 recovery by the seven experimental animals is traced for the first 11 days after their restoration to ad libitum conditions; the daily medians of the experimentals are compared to the combined control group data for the first three of these days and to their own base-line medians. Of greatest interest are the shifting trends in activity during the first few recovery days and the slow and very incomplete recovery of body weight.

Body weight. While the median weight of the control animals increases about 5 per cent during the experiment, the median weight loss of the experimentals during the deprivation phase is 31 per cent, the greater part of it occurring during the first 10 or 15 days. After 11 days of recovery the experimental rats are still 13 per cent below their original base, and 20 per cent below the reference median of the controls.

Food and water intake. There is no consistent trend among the control rats in amount of food and water ingested. As would be expected, the food intake of the experimental animals during the daily feeding hour is least during the first five days of deprivation, increasing gradually as they learn to compress their eating time and as the total deficit accumulates. By about the twentieth day an asymptote of 60 per cent of base (or 55 per cent of the control median) seems to be approximated; it is interesting to note that this is also the point beyond which there is relatively little decline in body weight. The self-imposed water restriction is irregular, and is in general less severe than the food reduction (cf. 2). On the first day after return to unlimited feeding the food intake comes back to base line and the water intake far overshoots. Thereafter both are above normal for the balance of the recovery period.

Activity. The 24-hr. activity of the control animals varies within a range of 200 revolutions, with a slight downward trend discernible. The activity of the experimental group, by contrast, rises to a peak of 1074 per cent of base during the third five-day period of restricted feeding, drops somewhat in the next five days, and then increases gradually to a final maximum of 1352 per cent. Variation in individual records is too great to confirm this pattern unequivocally, but five of the seven curves are characterized by the double inflection, and four reach their highest point during the last ten days of deprivation.

The most clear-cut and consistent change is in the activity during the hour just preceding the daily feeding. While the control median never exceeds one revolution, the median of the experimental group rises from the zero base line to 60 revolutions during the first five deprivation days, and in the succeeding periods increases without interruption to 1671. With only minor deviations the individual data reflect this group trend. Without exception every rat's activity is higher in the seventh 5-day period than in any other, and there is no indication that an asymptote is being approached. According to this index, adjustment to the 23-hr. feeding schedule is incomplete at the end of 35 days.

Activity during the recovery phase follows a somewhat more complex pattern. Total activity is on the first day 61 per cent below the base line (the "satiation syndrome" [1]), rises above base for a few days, and then drops back within the normal range. Meanwhile the activity in the hour corresponding to the prefeeding hour drops below any point observed during the deprivation phase, increases unmistakably for two days, and then gradually decreases to zero.

DISCUSSION

The question which the experiment seeks to answer is quite straightforward: How long is required for a rat to adjust to a 1-hr.-per-day feeding schedule, so that the progressive upward trend of motivation resulting from cumulative deficit will level off? How soon can the animal be introduced to daily trials in, for example, a maze-learning situation without danger of distortion of results by a continuing elevation of drive state? The answer must be given in several parts. Each of the measures used indicates that 15 days is the irreducible minimum for adjustment to the limited feeding regime. Up to this point, weight has steadily declined, ingestion has not leveled off, and the activity has increased tremendously. This much finds confirmation in the 24-hr. activity data of Hall *et al.* (3), which show a distinct rise for at least 12 to 17 days. Beyond 15 or 20 days, however, our measures diverge. Further changes in weight and ingestion are relatively small, and 24-hr. activity temporarily decreases. But the activity in the last prefeeding hour continues to increase. By this evidence, even a 35-day period is too short for adequate motivational adjustment to this feeding schedule to occur.

It may be, of course, that the continuing increase in the activity of the prefeeding hour is a reflection of something other than progressively increasing primary drive. It could be argued that during the first 15 days of feeding cycles, heightened motivation (indicated by weight loss and increased rate of eating) leads to an increase in activity during all periods of the day. But the responses occurring in the hour just before presentation of food would be most strongly reinforced, due to temporal proximity to the feeding, and would for this reason tend to increase still further in frequency or amount on successive days. By this process, the activity in the last hour could continue to rise for many days after the hunger drive characterizing that hour had reached its asymptote.

Examination of the activity data during recovery lends some support to this notion of an acquired running increment. We may assume that on the first day of free feeding the running habit is strong, but that its performance is inhibited (paralleling the satiation syndrome that is signaled by the subnormal total activity for the day). In the next two days the satiation syndrome diminishes (suggested by the high total activity level), and the habit is free to express itself in increased running during the hour. Then, because these particular responses are no longer reinforced differentially, extinction gradually occurs, the depressing effect of light once more asserts itself, and the activity of the hour drops to zero.

Whether the progressive increase in prefeeding activity over the 35 days is due primarily to increasing hunger drive or to increasing habit strength, it suggests a methodological complication in certain experimental designs. To the extent that such a trend occurs in an experiment involving extended deprivation cycles, the effect of the manipulated variables may be subject to serious distortion.

It might be argued, of course, that there are certain critical differences between our experiment and others utilizing feeding cycles. For example, it may be that the rat is more active in the wheel than it would be in an ordinary living cage, that more body tissue is burned up in this activity, and that the cumulative deficit is hence more severe and more greatly prolonged than under other circumstances. Further investigation is required to test this possibility, and to examine the relative roles of learning and increased motivation in the elevation of activity during the 35 days of observation.

SUMMARY

The adjustment of seven rats to 35 days of 23-hr. food-deprivation cycles was measured in terms of body weight, food and water intake, 24-hr. activity (revolving wheel), and activity during the last prefeeding hour. Comparison with a control group reveals that progressive changes in all measures continued for at least 15 days, and that activity during the hour immediately prior to feeding was still increasing at the end of the 35 days.

It is possible that similar trends constitute an unrecognized source of error in other experiments involving daily feeding cycles.

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QUANTITATIVE CONTROL OF MOTIVATION THROUGH SUCROSE SOLUTIONS OF DIFFERENT CONCENTRATIONS

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The present study is the outgrowth of previous studies (4, 5) in which it was found that rats prefer the higher concentration of two sucrose solutions (presumably the sweeter solution). The former studies suggested to us the possibility of controlling the degree of motivation by varying the concentration of solution. Animal trainers have long used sugar lumps as rewards in the training of their *Ss*, but for laboratory purposes it is desirable to have a quantitative control over the *value* of the reward. The concentration of solution offers such control with precision far greater than that required for any conceivable psychological work.

Not only can the concentration be controlled but the duration of contact with the solution can be varied. In the previous study, we limited rats to 1 or 4 or 16 contact-seconds, but in the present work we have limited the animal's reward to 1 contact-second per day with the test solution.

The work was carried out with healthy rats that had an unlimited supply of an adequate food and tap water continuously present in their cages. There was no known deprivation or metabolic need of any kind. Rather than to create distress through deprivation, we rewarded the animals with a positively acceptable sweet-tasting fluid that supplemented their usual, fully adequate diet. The problem that we studied was a typical one: learning to run down a runway from starting box to the sugar solution in the goal box and the extinction of the running habit after it had been acquired.

METHOD

Rats were timed as they ran down a runway from starting box to goal box, over a minimal distance of 6 ft. At the far end of the goal box was a glass cup (⅞-in. inside diameter) containing a sugar solution. Each rat made a single run per day and was rewarded by 1 sec. of contact with the sugar solution. The daily run was preceded by a 60-sec. delay in the starting box and followed by a 60-sec. delay in the goal box. The experimental variables were: (*a*) The concentration of sugar solution offered as a reward, and (*b*) the number of daily runs.

Experimental Plan

The experiment as a whole was divided into two parts—the first concerned with acquisition of a running habit and the second with resistance of the habit to extinction after removal of the reward. After preliminary experience with a sugar solution, as described below, each rat was given one run daily for 25 days. This period of learning, or acquisition, was interrupted by a 16-day pause after day 19 (Christmas vacation); the pause gave opportunity for forgetting and relearning of the running habit.

On day 26, the sugar solution was removed from the cup and distilled water substituted. There were 21 days of running in the series concerned with resistance to extinction. For the first 15 of these days the rats ran to a cup filled with distilled water and for 6 additional days to an empty cup. During extinction the experimental conditions were held constant except for the change in contents of the cup.

Apparatus

The runway was made of gray-painted wood, covered with hardware cloth. Its over-all length was 7 ft., including a 1-ft. starting box, a 5-ft. mid-section, and a 1-ft. goal box—the starting box and goal box being continuous with the mid-section. Starting box and goal box were equipped with sliding doors for controlling approach to the goal and to prevent retracing. The cross section of the runway was 4⅛ in. wide by 3¾ in. deep. In an actual run the minimal distance to be covered was 6 ft., i.e., the distance from the threshold of the door of the starting box to the center of the foodcup at the far end of the goal box. A glass foodcup mounted to a disk upon a sliding rod was so arranged that the cup could be lowered out of reach of the rat, through a hole in the floor whenever *E* pressed a key.

Two timers were used in the experiment: (*a*) A standard timer for measuring, in hundredths of a second, the over-all running time between lifting of the door to the goal box and contact of the animal with a sugar solution. (*b*) A cumulative timer for limiting the rat's contact with the solution to 1 sec. and for taking time out if the rat stopped drinking to explore

Procedure

On each daily run the rat was first placed in the starting box. After a 60-sec. delay the door to the starting box was raised and the timer started. At the instant the rat made contact with the sugar solution the timer was stopped, thus measuring the total time spent by a rat in the box and runway prior to contact with the sugar solution. Actually we measured separately the time the animal delayed in the box (latency) and the time he required to run from the threshold of the door to the sugar solution (running time), but since these partial measures tell essentially the same story as the total running time, we are basing the present report solely upon the total, or over-all, running times. At the same instant, *E* pressed a telegraph key that started the cumulative timer; he released this key whenever the rat paused to look around or to explore. When a total contact of 1 sec. had been accumulated, there was a sharp buzz to which *E* responded by removing the cup. After this, there was a 60-sec. delay in the goal box before the rat was removed.

Rats

The *Ss* were 16 albino rats, 8 of each sex, 65 days old at the start of the experiment and 130 days old at the close. The rats were assigned to four weight-equivalent groups each containing 2 males and 2 females. For clarity and convenience, we will designate the groups by numbers that correspond to the concentrations of sugar solutions offered as reward to the members of a group. Thus, the four groups are labeled, respectively, as groups 2, 6, 18, and 54.

Preparation and Care of the Solutions

The four concentrations of sucrose solution—2, 6, 18, 54—are the same as those used in the previous experiment. The four concentrations form a geometric sequence obtained by successive multiplication by 3. Thus, they are equally spaced on a logarithmic scale. All solutions were prepared and their concentrations specified in terms of percentage by weight, i.e., a 2 per cent solution contained 2 gm. of sucrose and 98 gm. of distilled water per 100 gm. of solution. Solutions were prepared from pure commercial cane sugar (sucrose) of high quality; they were kept at room temperature (constantly at 78°F.) in storage bottles. Fresh solutions were mixed from time to time.

Preliminary Experience with the Sugar Solutions and Runway

Prior to the main experiment each rat was allowed a total of 75 contact-seconds with the particular sugar solution to be used as an incentive. The first 60 sec. of contact with the solution were on another apparatus (the preference tester with a single cup). After this, on two successive days, groups of rats were placed in the runway and allowed to explore the apparatus for a total of 100 min., no sugar solution being present. Finally, each rat individually was placed in the goal box with its door closed and was allowed to accumulate 15 contact-seconds with the sugar solution to be used as an incentive.

RESULTS

The raw data for the experiment are measurements of time elapsed between raising of the door to the starting box and first contact of the animal with the test fluid. The raw data have been transformed into measures of *speed* (feet per second) by dividing the minimal distance covered (6 ft.) by the total running time (in seconds). Then, to smooth off the curves, we obtained the average speed for three successive days (except that interval 6 in the acquisition series was an interval of four days). Thus, each average speed of locomotion, plotted as a point on a curve, is generally based upon 12 time measurements (four rats, three days). Results for the four groups, of course, are plotted separately.

The average speed of locomotion for successive three-day intervals is presented graphically in Figure 1. The figure as a whole has two main parts corresponding to the two main divisions of the experiment. During the first part of the experiment the rats made a single run per day down the runway to a reward consisting of a sugar solution which each animal sipped for one cumulative contact-second. The first three days with distilled water following the acquisition series are counted as the first three-day interval in the second part of the experiment concerned with extinction. The transition between acquisition and extinction is indicated on the graph by dotted lines. The

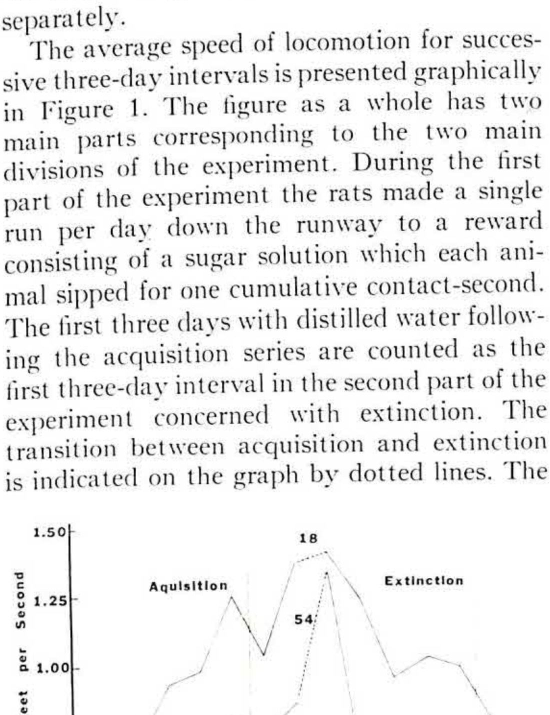

FIG. 1. Acquisition and extinction of a running habit as related to concentration of sucrose solution offered as reward (16 rats, 4 per group). The vertical line between intervals 6 and 7 of the acquisition series indicates a 16-day pause in the experiment during the Christmas vacation. The vertical line between intervals 5 and 6 of the extinction series indicates a change from an incentive of distilled water to an empty cup. Numbers on the graph indicate concentrations of solutions.

experiment was continuous, however, there being no break in the daily runs when distilled water was substituted for sugar solution. All conditions, except the change from solution to distilled water, and later to an empty cup, were held constant throughout the experiment.

The two vertical lines on Figure 1 need a word of explanation. The line between intervals 6 and 7 of the acquisition series indicates a 16-day pause at the time of the Christmas holidays. The line between intervals 5 and 6 during the extinction series indicates a change from distilled water to an empty cup. Numbers on the graph refer to concentrations of sugar solution offered as a reward to groups of rats.

DISCUSSION

Figure 1 shows that all groups gained in speed of locomotion with practice. The rats of group 18 (perhaps by chance) were the fastest at the start of the experiment and they maintained their superiority throughout. Although rats generally prefer the higher concentration of two sucrose solutions, this preference is not revealed by the graphs for groups 18 and 54, nor is the preference for the higher concentration revealed by the curves for groups 2 and 6. It is clear from Figure 1, however, that the curves for the two higher concentrations (18 and 54) are consistently higher than those for the two lower concentrations (2 and 6).

To study the statistical significance of group differences, we have limited consideration to the last five days of practice in the acquisition series and we have compared the groups by using a nonparametric test (Mann-Whitney *U* test). The results are shown in Table 1. These figures show, as we might expect on the basis of the curves in Figure 1, that the differences between groups 6 and 18, and between 6 and 54, are significant, while the difference between groups 2 and 18 is almost significant. It would require larger groups of animals to rank the concentrations in order of effectiveness with statistical certainty. In any event the figures show that speed of locomotion is significantly related to the concentration of the sugar solution used as an incentive, even though they do not demonstrate a one-to-one relation between speed of locomotion and concentration of solution.

TABLE 1
Significance of Group Differences (p) During Last Five Days of Practice in the Acquisition Series

Group	Group		
	2	6	18
6	.443		
18	.057	.029	
54	.171	.029	.343

The interpretation of this lack of a one-to-one relation between speed of locomotion and concentration of solution is a matter to discuss. It is conceivable that the rate of running is *not* a monotonic increasing function of the concentration. Guttman (2), in a bar-pressing experiment, reported that with *continuous* reinforcements (each taste consisting of about .005 ml. of sucrose solution) the relation between rate of bar pressing and concentration of solution ceased to be monotonic after about 100 tastes, and there was a maximal rate of responding at about 16 per cent. With *periodic* reinforcements, however, the rate of responding was an approximately logarithmic increasing function of the concentration. Under our present conditions we would expect the rate of running to be an increasing monotonic function of the concentration, as with Guttman's periodic reinforcement of bar pressing. We believe that the inversions in our results are bound up with chance variations. There were only four rats in each of our groups, and with larger groups of animals the expected relations might be obtained as they were in our earlier study (5).

We are inclined, however, to the following interpretation. In general, rats run faster to the preferred of two foods, but another study (3) indicated that the speed of running is not a reliable criterion for the prediction of food preferences. This is because running speed depends upon many factors; it is known to vary with size and age of rat, state of health, endocrine balance, dietary need, estrus, previous training, as well as with the value of the incentive as shown by tests of preference. These many factors that affect running rate produce variability in the results. It is not known how effective the incentives can be in relation to other factors that regulate performance, but results shown in Figure 1 demonstrate that incentive control can and does make a great difference in speed of locomotion.

In the first part of the experiment, between intervals 6 and 7, there was a 16-day gap in the running during which all groups fell to a lower level of performance. Following the period of normal forgetting, there was relearning with three of the groups. Group 2 showed no relearning. In the previous study (5), we found that a 2 per cent sugar solution yielded sporadic periods of learning interspersed with periods of nonlearning. A 2 per cent sucrose solution is not far removed from the hedonic threshold of learning (cf. Guttman's concept of "threshold of reinforcement").

It will be observed that all animals showed an increase in speed of locomotion between the last three-day interval of the acquisition series and the first three-day interval of the extinction series. The initial increase was followed by a lowering of speed to the original performance level for group 54 and to points below the original performance level for groups 2 and 6. Group 18, the fastest of all, had not reached the original running level at the time the experiment was terminated. Actually, groups 2 and 6 were the first to reach their original levels of performance; then group 54; and, if the experiment had been continued, group 18 would necessarily be the last to reach its original level.

Why was there an initial rise in the level of performance immediately after the sucrose solution was removed and distilled water substituted? Our hypothesis is that a change from sugar solution to distilled water (no sugar at all) is frustrating to the expectations of the rats based upon their previous experiences. Frustration, we assume, increases the proprioceptive tension of the preparatory set over and above the tension level already existing from the frustration of having to delay for 60 sec. in the starting box prior to a run.

In this connection, we pause to point out that Crespi (1) appealed to frustration in the interpretation of his results. He reported changes in the speed of running associated with shifts in the magnitude of reward (from 16 pellets to 1 or to 0 pellets). Although Crespi's findings and interpretations do not agree with ours in detail, we are interested to note that he appealed to frustration of the expectations of the rats when explaining results.

If we pay attention to the slope of the curves of extinction as presented in Figure 1 and if we measure the slope between intervals 1 and 5 (the first and last with distilled water), we will observe that the curve for group 54 has the steepest slope and the curve for group 18 is next in steepness of slope; then comes group 6, and finally group 2 with the least steep curve. In other words, the steepness of slope between intervals 1 and 5 varies inversely with the concentration of solution that was presented as a reward during the learning series. The change from distilled water to an empty cup on intervals 6 and 7 does not change the relative steepness of the slopes of extinction curves. This finding agrees with data presented graphically by Guttman (2). His curve (Fig. 3) shows that the steepest decline in rate of bar pressing is for the highest concentration and the least steep decline is for the lowest concentration that was presented during conditioning.

CONCLUSIONS

1. Well-nourished rats that are neither hungry nor thirsty approach a sucrose solution, after several daily 1-sec. contacts with it, at a speed of locomotion that varies directly with the concentration of solution. The speed of locomotion, however, is not a very reliable criterion for the estimation of relative values among the test solutions. More consistent appraisals of relative value can be made with preference tests.

2. The rate of running to a sucrose solution is dependent upon the number of previous contacts with it as well as upon the concentration of solution used as a reward.

3. If distilled water is substituted for sucrose solution after the habit of running down a runway has been learned, there is an initial increase in speed of locomotion followed by a steady decline. The initial increase in speed is interpreted as a result of increased proprioceptive tension when the expectations of the animals are frustrated.

4. The steepness of the curves showing resistance to extinction varies inversely with the concentration of sucrose solution originally offered as a reward in the learning series. Also, the rats running to the lowest concentrations

of sucrose solution reached their original level of performance prior to those running to the highest concentrations.

5. The experiment as a whole demonstrates that the degree of motivation can be adequately controlled in normal, well-nourished rats, without any deprivation, through control of the concentration of sucrose solution that is offered as a reward when the animal's contact with the solution is limited to a single second per day. Motivational control through scaled incentives appears to be feasible for experimental work upon learning and forgetting, resistance to extinction, frustration, and related psychological phenomena.

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CORTICAL TASTE MECHANISMS STUDIED BY TWO DIFFERENT TEST PROCEDURES

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In a previous paper (2) it was demonstrated that ablation of the cortical receptive zones for the chorda tympani and IXth nerves produced lasting increases in quinine thresholds as measured by the two-bottle preference method. Further, single-stage ablation of essentially all the neocortex lying outside this region had no measurable effect. This, however, provides only partial information about the role of this area in the discrimination process. The generalization that this area is concerned in taste discrimination, per se, without reference to the method of measurement is not warranted. The purpose of the present experiment is to investigate the effects of ablation of this area on taste thresholds as determined by another method.

The one-bottle or single-stimulus method was originally introduced by Beebe-Center, Black, Hoffman, and Wade (1948). In this method the animal is presented with one test fluid per day, the measure of preference or aversion being the difference between the amount of test fluid consumed and the amount of water normally consumed in 24 hr. A modification of this procedure restricts the test period to 1 hr. (3). The animal is deprived of water for 15 hr., given a 1-hr. test, then deprived for 2 hr., and finally, allowed 6 hr. with free access to water. In the study of aversion thresholds this arrangement would seem particularly advantageous, since the animal does not have to fulfill his daily fluid requirements from a solution which is normally (i.e., in a choice situation) avoided. For this reason the 1-hr. intake measure is utilized in the present experiment.

METHOD

There were five essential steps in the experiment: (*a*) Determination of the two-bottle threshold for quinine hydrochloride ($N = 16$), (*b*) determination of the one-bottle threshold for quinine hydrochloride ($N = 16$), (*c*) rest period eight days (control group, $N = 6$), operation and recovery period eight days (experimental group, $N = 6$), (*d*) postoperative one-bottle threshold determination, (*e*) postoperative two-bottle threshold determination.

Male albino rats, three to four months of age, were used. Their eyes were enucleated before any tests were conducted. This procedure was necessary as a control for possible damage to the optic blood and nerve supply during subsequent cortical operations. Each animal was housed in an individual cage to the front of which could be fastened one or two 100-cc. graduates equipped with rubber stoppers and matched drinking tubes. The experiment was conducted in an air-conditioned room with a constant temperature of 70° F. ± 4°.

In determining the two-bottle thresholds a given concentration of solution was presented for a total of 48 hr., the position being determined by a double-alternation sequence. That is, the solution would be placed in the left bottle for 24 hr., then the right for the same period. The next concentration started on the right, then the left, etc. The position of the bottles and drinking tubes remained constant. By this procedure position habits and extragustatory cues were controlled.

A descending series of molar concentrations of quinine hydrochloride (QHCl) was used, as follows: .00008, .00003, .00002, .000008, .000003, .000002, .0000008. The threshold was defined as the last concentration at which the quinine intake constituted less than 25 per cent of the total fluid intake.

The one-bottle thresholds were then determined. The 24-hr. schedule for the one-bottle tests is indicated below:

Period	*Time (Hr.)*	*Fluid*
Test	1	Tap water or QHCl solution
Rest	$1\frac{1}{2}$	None
Free access	$5\frac{1}{2}$	Water
Deprivation	16	None

Food was available at all times. After a five-day adaptation period when only water was presented during the test period, quinine solutions and water were presented on alternate days. Threshold was defined as the lowest concentration at which the test-period intake of quinine solution was less than the water intake on the preceding or following test periods.

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[1] This research was carried out while the author held the R. G. D. Richardson Fellowship, Brown University, 1952–1953. The study was part of the writer's dissertation presented to the Graduate School of Brown University as partial fulfillment of the requirements for the Ph.D. degree. The author wishes to express his appreciation to Dr. Carl Pfaffmann for his assistance throughout the course of the investigation.

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TABLE 1

Pre- and Postoperative Quinine Hydrochloride Thresholds (Molar × 10^{-6}) as Measured by the One-Bottle, 1-Hr. and the Two-Bottle, 24-Hr. Methods

Animal No.	Preoperative		Postoperative	
	Two-Bottle	One-Bottle	Two-Bottle	One-Bottle
127	30.0	20.0		
128	8.	30.	30.0	20.0
132	8.	30.	8.	30.
140	20.	3.		
141	80.	80.	200.	30.
142	2.	8.	20.	8.
143	8.	80.		
144	20.	20.	80.	8.
145	8.	80.		
146	3.	80.	80.	30.
147	8.	8.	8.	3.
148	20.	30.	8.	20.
149	20.	200.	30.	80.
150	80.	200.	30.	80.
151	8.	80.	8.	30.
156	20.	30.	8.	30.

TABLE 2

Postoperative Threshold Changes for the Experimental and Control Animals on the Two- and One-Bottle Tests

Animal	Two-Bottle	One-Bottle
	Experimental Group	
146	26.7	0.38
142	10.0	0.00
144	4.0	0.40
128	3.8	0.67
141	2.5	0.38
149	1.5	0.40
	Control Group	
132	0.00	0.00
147	0.00	0.38
151	0.00	0.38
148	0.40	0.67
156	0.40	0.00
150	0.38	0.40

The same descending series of molar concentrations of quinine hydrochloride used in the two-bottle determinations was employed here. In two cases this was below threshold on the one-bottle test and a .0002-M. solution was introduced.

The cortical area was exposed by means of a trephine hole in the posterior orbital surface of the skull. Ablations were carried out by aspiration under Nembutal anesthesia. Penicillin was administered on the first two postoperative days. The lesions were made comparatively large to assure that the whole composite nerve area was removed. The area was constructed from the maps of six evoked-potential recording experiments utilizing electrical stimulation of the IXth and chordatympani nerves (2).

Following the postoperative tests the animals were drowned, the brains fixed in 10 per cent formalin and embedded in paraffin. Serial sections (25 microns) were obtained for the entire cerebrum. One section every 250 microns was stained with thionin. Camera lucida tracings of these cross sections were used to plot the lesions on standard Lashley diagrams.

RESULTS

Preoperative Thresholds

The preoperative thresholds expressed in molar concentrations are presented in the first two columns of Table 1. The Wilcoxon (1949) test for paired replicates indicates that the one-bottle thresholds are significantly higher than the two-bottle thresholds ($p < .02$).

Postoperative Thresholds

The postoperative molar thresholds are presented in the last two columns of Table 1. In order to facilitate comparisons these thresholds have been expressed in terms of the relative change from each animal's own preoperative threshold. In the case of animal 146, for example, the preoperative two-bottle threshold was 3×10^{-6} M., postoperative, 80×10^{-6} M., an increase of 26.7 times. The preoperative one-bottle threshold for the same animal was 80×10^{-6}, postoperatively, 30×10^{-6}, or .38 times his preoperative level. These threshold changes are presented in Table 2.

The following generalizations can be made:

1. The postoperative thresholds for the control group either remained the same or decreased on both the one- and two-bottle tests.
2. The thresholds for all the experimental animals increased postoperatively on the two-bottle test, but decreased or remained the same on the one-bottle test.

The two-bottle threshold changes for the experimental group are significantly different ($p < .01$) from those of the control group (Wilcoxon unpaired replicates).

Histological

The lesions in all animals destroyed all the receptive areas bilaterally (Fig. 1) with no sub-

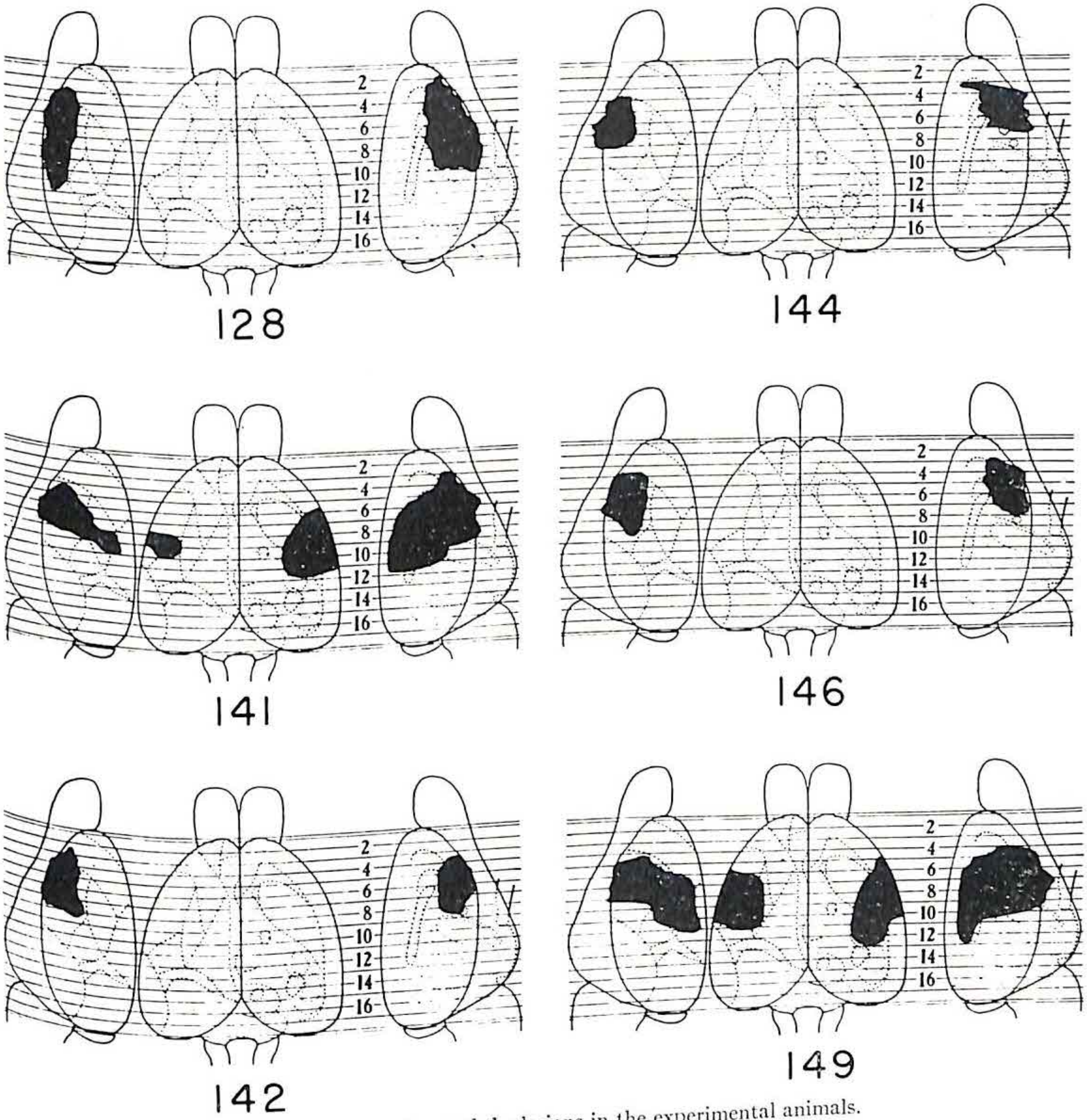

FIG. 1. Reconstructions of the lesions in the experimental animals.

cortical damage except for the lateral tips of the corpus callosum in some cases. There is no relation between the size of the lesion and the magnitude of the two-bottle deficit.

DISCUSSION

Several data point to the conclusion that gustatory discrimination as displayed in these two situations is not a unitary process. First, the normal thresholds determined by the two different methods are significantly different. Secondly, ablation of the nerve receptive areas produces deficits in the two-bottle, but not in the one-bottle, thresholds. There appear to be two factors in the experimental situations which could account for this: the arrangement of the stimuli (one vs. two bottles) or the fluid deprivation state (16 hr. vs. none). Correlated with a deficit are two bottles and low deprivation; with no deficit, one bottle and high deprivation.

The available evidence gives little indication as to the relative importance of these factors. Presumably this could be tested with two additional experimental situations: a two-bottle, high-deprivation test to be compared with the present two-bottle, low-deprivation test and a one-bottle, low-deprivation test as opposed to the present one-bottle, high-deprivation test.

In the absence of definitive data the following interpretation is tentatively advanced. The second factor, fluid deprivation, is assumed to be the important variable. Therefore, it would be predicted that under low fluid deprivation an operated animal should show deficit regardless of the stimulus arrangement. More specifically, an animal with a deficit on the two-bottle, 24-hr. test should also have a deficit on a one-bottle, 24-hr. (i.e., low-deprivation) test. Conversely, the operation should not produce a deficit provided the animal is under high fluid deprivation. Thus, an animal with a deficit on a two-bottle, 24-hr. test should show no deficit on a two-bottle, 1-hr. (i.e., high-deprivation) test.

CONCLUSIONS

1. The quinine thresholds as measured by the one-bottle, 1-hr. method are significantly higher than the two-bottle, 24-hr. thresholds.

2. Ablation of the cortical receptive area for the IXth and chorda tympani nerves, which increases the two-bottle, 24-hr. thresholds, has no effect on the one-bottle, 1-hr. thresholds.

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THE EFFECTS OF ETHER AND A BARBITURATE ON WATER REGULATION IN THE RAT[1]

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Laidlaw and Kennard (4) have noted the somewhat specific action of the barbiturate, Dial (diallybarbituric acid), on the blood vessels of the hypothalamus and of the cerebral cortex in monkeys, the effect being one of vasodilatation of the former and vasoconstriction of the latter. Fulton, Liddell, and Rioch (1) have reported a specific pharmacological affinity of the barbiturates for the hypothalamus. In the course of a number of experiments in our laboratory we have observed an extremely reliable depressing effect on water ingestion in rats following light anesthetization with ether, whose vascular action is just the opposite to that of Dial, producing cerebral vasodilatation and hypothalamic vasoconstriction (4). Jones (3) reports a significant increase in water intake of rats receiving daily injections of phenobarbital. Heller and Smirk (2) studied the effect of anesthetic dosages of ether, chloroform, luminal, paraldehyde, urethane, and chloralose on the intestinal absorption and excretion of water loads in rats deprived of water for 24 hr. They found intestinal water absorption to be markedly delayed by ether and chloroform. There was also an inhibition of diuresis even when time for water absorption was allowed before induction of anesthesia. The hypnotics used had a slight inhibiting effect on absorption but no effect on diuresis.

Preliminary observations in our laboratory having shown that water intake appeared to be increased by preingestional injections of subanesthetic dosages of Dial, it was possible to design experiments to test the degree of association between ingestion and diuresis without a direct manipulation of serum electrolyte concentrations. In the experiments to be reported, the first is concerned with establishing the effects of ether and Dial on the water intake of 23-hr. water-deprived rats, and the remainder are observations of the effect of ether and Dial on the antidiuretic responses of satiated and water-deprived animals.

EXPERIMENT I. THE INFLUENCE OF ETHER AND DIAL ON WATER INGESTION

Procedure

Twelve male albino rats 100 days of age at the beginning of the experiment were adapted to a 23½-hr. water deprivation for 10 days. By the end of this period the daily ½-hr. water intake and body weight had stabilized. The animals were assigned to three groups equated on the basis of water intake in the last 5 days of the adaptation period. The experimental design was a replicated latin square in which all animals received all four conditions: predrink etherization, predrink subcutaneous injections of Dial, etherization control condition, and Dial control condition. Each day of application of an experimental condition was followed by 3 days of 23½-hr. water deprivation and ½-hr. drinking, a procedure necessary to minimize residual effects of a particular day's treatment.

The four experimental conditions were administered as follows:

Etherization. A cylindrical glass museum jar, 253 mm. in height and 220 mm. in diameter, the bottom covered with wood shavings and the top with plate glass, was used. The shavings were saturated with ether, and the animal was placed on a circular hardware cloth platform 90 mm. above the bottom of the jar. The animal was left in this atmosphere, which approached saturation for ether vapor, until it showed complete cessation of front limb and neck muscle activity. The actual behavioral criterion dictated that the animal be removed when it fell on its side and made no further efforts to right itself. While there was some variability from animal to animal, the mean time in the chamber was approximately 65 sec. Following removal from the chamber the animal was placed in a drinking box of the type described in an earlier report (6) and allowed, after a 15-min. delay, access to water for ½ hr. In this period of time the animals uniformly showed complete skeletal muscle recovery from the anesthetic and were maintaining an alert and active orientation toward the door separating them from the drinking tube.

Ether control procedure. A museum jar, identical with that used for etherization, was employed. Animals were placed in this jar for 65 sec., removed, and placed in the drinking box, where the length of delay and drinking period was identical with that used in the preceding condition.

Dial procedure. The animal received a subcutaneous injection of 20 mg/kg body weight of Ciba Dial (0.1 gm/cc of diallybarbituric acid) and was immedi-

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[1] This research was supported and made possible by funds from the Graduate Research Board of the University of Illinois.

ately placed in the drinking box and delayed as in the preceding conditions.

Dial control procedure. The animal received a subcutaneous injection of physiological saline equal in volume to its corresponding Dial dosage. It was then placed in a drinking box and subjected to the same procedure used in the other conditions.

Results

The variances of the three squares showing homogeneity by Bartlett's chi-square test were combined, yielding a treatment effect significant beyond the .01 level. The mean water intakes in cubic centimeters under the ether, Dial, ether control, and Dial control conditions were 16.1, 23.8, 19.0, and 19.6, respectively. The ether-Dial and ether-ether control differences are significant beyond the .01 level; the Dial-Dial control difference was significant at the .05 level of confidence. It appears justifiable to conclude that preingestion dosages of ether and Dial influence water consumption in opposite directions.

EXPERIMENT IIA. THE INFLUENCE OF ETHER AND DIAL ON DIURESIS OF 23½-HR. DEPRIVED ANIMALS

Procedure

Twelve male albino rats approximately 120 days of age were adapted to a 23½-hr. water deprivation schedule for 10 days and then assigned to 3 groups equated as in Experiment I. The experimental design was also similar, being three latin squares in which each animal received ether, Dial, ether control, and Dial control conditions exactly as in Experiment I, and with the same 3-day interval between successive tests. Two variant diuresis tests were used. In Procedure A, the animal was wrapped in a towel, the mouth spread by forceps, a no. 10 French catheter inserted, and a 4 per cent body weight load of water was administered. Immediately following placement of the load, the Dial experimental condition was applied. The ether animal was lightly anesthetized, delayed 10 min., and then loaded. Each animal was then placed in an individual metabolism cage, and urine output was recorded at 10-min. intervals for 4 hr. The metabolism cages consisted of a circular hardware cloth container 160 mm. high and 200 mm. in diameter, the top of wood and the bottom of hardware cloth, placed on glass funnels 240 mm. in diameter. Two fine-gauge copper screens were interposed between the cage and the throat of the funnel. The urine was collected in centrifuge tubes which fit closely around the funnel stem. Sham runs in which known quantities of water were allowed to drip through the cage showed constant retentive and evaporative conditions between the various cages. Four animals were used in this procedure.

In Procedure B the animals were placed in individual drinking boxes and allowed to drink a volume of water equivalent to 4 per cent of their body weight. They were then given the experimental condition and placed in the metabolism cages. Eight animals in two squares were used in this procedure.

Results

The analysis of variance on total urine for Procedure A and Procedure B showed no significant effect of treatment for either procedure. It is clear that neither ether nor Dial, in the amounts to which our animals were exposed, have measurably differential effects on urine excretion.

EXPERIMENT IIB. THE INFLUENCE OF ETHER AND DIAL ON DIURESIS IN NONDEPRIVED ANIMALS

Because the animals in the preceding experiment were in a state of negative water balance at the time of their diuresis test, it could be argued that the 4 per cent body weight load of water was enough less than their water deficit (mean of 5 to 6 per cent of body weight) to obscure any differential effect that ether or Dial might have on water clearance. Accordingly, in the present experiment, animals in a state of water balance were employed.

Procedure

Eight male albino rats approximately 120 days of age were used. They were maintained on continuously available food and water. Two groups of four animals each were formed, the animals being assigned in terms of matching body weights. Ether, Dial, and the two control conditions were applied in the same manner as previously described. The 4 per cent body weight water load and test conditions were applied every fourth day. Food was removed from the cages 14 hr. before each test.

Results

The combined analysis of variance again showed no significant treatment effects. Although greater volumes of urine were recovered, there was no differential diuretic effect produced by the experimental conditions. Analysis of the proportion of load excreted 1, 2, and 3 hr. after loading likewise revealed no differences between the various experimental conditions.

DISCUSSION

These experiments demonstrate that small dosages of ether serve to decrease water ingestion of dehydrated rats and that small dosages of Dial slightly enhance ingestion by the animals. They further show that these opposed ingestional effects occur in the absence of measurable differences in diuretic regulation of water. If the findings we have reported are valid, it is possible to suppose that the two aspects of water regulation, ingestion and excretion, may be independently manipulated, and thus are separate, though usually synchronized, mechanisms.

The opposed effects of ether and Dial on ingestion pose, but do not answer, the question of how the influence is exerted. Dilatation of the vascular supply of the hypothalamus by Dial and vasoconstriction by ether may well produce changes in the sensitivity of the "osmoreceptors," the Dial-induced condition mimicking "dehydration" cues past the usual critical plasma dilution, and the ether-induced constriction exerting an effect in the opposite direction. In this connection, Leifer and Grinker (5) found that a higher intensity of stimulus is required to elicit hypothalamic responses under Dial than under ether. Another possibility, more susceptible to experimental test, is that ether and Dial may have opposite effects on stomach-emptying time. From direct observations we have recently made on stomach clearance rates of dehydrated rats it appears evident that ether definitely delays stomach emptying. This could lead to more rapid stomach distention and serve as an inhibiting agent in this manner. Unfortunately for this hypothesis, what little data we have collected on Dial and stomach-emptying time indicate its effects to be in the same direction as that of ether.

It is difficult to reconcile our findings with those of Heller and Smirk (2). We failed to find differential inhibition of diuresis between experimental and control groups in any comparison and with three variant diuresis tests. It may be that inhibition of diuresis can be accompanied by inhibition of ingestional activity, but it is far more usual for antidiuretic responses to be accompanied by drinking responses, the adequate stimulus for each being identical.

It is worth mentioning that the rate of water intake of animals under the ether and Dial conditions does not vary in its initial stages. During the first 5 to 7 min. the animals are drinking, no differences are observable. The ether animal simply takes in less water in the later minutes of the drinking period, and the Dial animal takes in more than do the control animals. Thus, whatever the factors are that mediate the differences in intake, they appear to operate on the cutoff or terminal stages of intake rather than on the over-all ingestional process. This fact seems to minimize any explanation which assumes the ingestional effect to be a part of some general systemic reaction.

SUMMARY AND CONCLUSIONS

Male albino rats maintained on a $23\frac{1}{2}$-hr. water deprivation were administered ether or Dial or suitable control conditions for these drugs. They were then allowed $\frac{1}{2}$-hr. drinking periods. Ether was found to depress drinking and Dial was found to enhance drinking. Diuresis tests of dehydrated and hydrated animals under these experimental conditions showed no differential diuretic effect on the dosage levels of ether or Dial administered.

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FRONTAL LOBOTOMY AND THE ELIMINATION OF CONDITIONED ANXIETY IN THE RAT[1]

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It has become a common practice to treat cases of extreme anxiety in the human being by means of cerebral prefrontal lobotomy. The meliorative effects of lobotomy proper are, nevertheless, but poorly known and understood. In these circumstances, one is inclined to turn to comparative data in order to reach an understanding and evaluation of the operation.

There is not, among the comparative data, a great deal of quantitative, experimental evidence to support the intuitive conviction that lobotomy itself reduces anxiety. Lichtenstein (8, 9), using dogs, has demonstrated rather clearly that a shock-instilled inhibition of the feeding response can be greatly reduced by prefrontal lobotomy. On the other hand, however, Kahn (7) failed, as did Streb (10), to obtain evidence that lobotomy is effective in reducing anxiety in the rat. When one notes, finally, that Brady and Nauta (3), in their investigation of a related problem, found that lesions of the septal forebrain in the rat tended to abolish fearful behavior, one has fairly well reviewed the literature. By way of comparison, there is a considerable body of evidence on the efficacy of the allied clinical procedure of electroconvulsive shock, evidence offered principally by Brady, Hunt, and their collaborators (cf. 1, 2, 5, 6).

The purpose of the study described here was to investigate further the relationship between lobotomy and anxiety. The experimental subject was the rat; the surgical procedure was that which can be most rigorously described, in the case of the rat, as frontal lobotomy; and the methods of training and testing were those developed by Brady and Hunt in their investigations of electroconvulsive shock.

METHOD

Apparatus

The principal item of apparatus was a black, wooden grillbox, provided with a hinged top and one transparent glass wall. Its floor measured $31\frac{1}{2}$ by 9 in., and its interior height was $16\frac{3}{4}$ in. The floor consisted of $\frac{1}{16}$-in. brass rods, running transversely and spaced $\frac{1}{2}$ in. apart. Every ninth rod was painted white, to divide the floor into seven $4\frac{1}{2}$- by 9-in. rectangles. The grill was wired for 110-v., 60-cycle alternating current. An electrical buzzer, powered by a 12-v. transformer, served as the source of the acoustical conditioned stimulus. Both the grill and the buzzer were operated by handswitches.

Subjects

The experimental *Ss* were 50 naive, male, Sprague-Dawley albino rats. The experiment was performed first with 24 animals, then replicated with another 26; however, each animal was 60 to 65 days of age at the beginning of its own experimental service.

Procedure

The animals were handled extensively before the first day of experimentation. Beginning with the first day, the following schedule was observed:

First day. Each animal was allowed to explore the grillbox individually for 15 min. The number of times the animal passed from one floor rectangle into another during minutes 2 through 4, and during minutes 9 through 11, was recorded. Also noted were any manifestations, during these periods, of crouching. Crouching, as distinguished from simple resting, involves these characteristics: rigidity of posture; deep, heavy respiration; flattening of the ears against the head; and the assumption of a stylized position, usually one in which the head is held low and the tail is raised above the floor. It is a response often considered typical of "anxiety," as is the immobility induced by a noxious stimulus.

Second day. The conditioning procedure began. Each animal again spent 15 min. in the grillbox. The buzzer was sounded during minutes 2 through 4, and, just before and just after the buzzer stopped sounding, a momentary shock was administered through the grill. The same routine was followed during minutes 9 through 11. Each animal thus underwent two conditioning trials. Records of motility and crouching were again kept for the two critical periods.

Third day. The procedure of the second day was repeated.

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[1] This report is based upon research for the master's thesis, performed by the first writer under the direction of the second, in The Psychology Laboratory of The Pennsylvania State University, 1954.

Fourth and fifth days. For some animals, conditioning trials were continued; for others, they were not. Conditioning trials were terminated for any given animal when, on two successive trials, the animal remained crouching all during the period in which the buzzer sounded (except for the initial 15 sec. of that period, during which time a brief startle response was common). In exception to this rule, an animal which reached the criterion in just three trials (i.e., in the two trials of the second day plus the first trial of the third day) was administered a fourth trial (i.e., the second trial of the third day). Thus, no animal experienced fewer than four conditioning trials.

Sixth and seventh days. To eliminate signs of generalized anxiety, the procedure of the first day was repeated on the sixth and the seventh. At the end of the seventh day, the animals were apportioned into experimental and control groups by the following method. They were listed in order, according to the number of conditioning trials sustained. Successive animals were then paired, and a toss of a coin decided which member of each pair was to be assigned to the experimental group and which to the control group. The members of the former group were to be lobotomized, and the members of the latter were to undergo sham operations.

Eighth and ninth days. All animals underwent surgery. For animals undergoing surgery on the eighth day, the ninth day was one of recovery; for the remaining animals, the eighth day was one of experimental inactivity. Surgery was performed under intraperitoneal Nembutal anesthesia. The dorsal aspect of the skull was exposed by means of surgical scissors and electrical cautery. A dental drill was then employed to enter the skull on the median line, halfway between the level of the eyes and that of the ears. If the animal being operated upon was an experimental animal, it was lobotomized by means of a small, specially fashioned leucotome which was inserted through the opening in the skull. If it was a control animal, it was not further invaded. In either case, the incision was finally dusted with an antibiotic powder and closed by interrupted suture. Post-mortem examination disclosed that the lobotomizing incisions lay, typically but with some variation, in a transverse section approximately one-third of the way between the frontal and occipital poles of the brain. The incisions extended over 50 to 90 per cent of the total area of this section, in most cases approaching the latter condition.

Tenth and eleventh days. All animals were allowed to recover from surgery. Of the 50 original *S*s, 10 did not survive. Fortunately, 5 of these came from each group. The remaining 20 animals in each group were reranked, and 20 new pairs were formed, on the same basis as originally. Inasmuch as nearly all the animals finally employed had sustained just four conditioning trials, the final matching was quite satisfactory.

Twelfth and thirteenth days. On the twelfth experimental day, each animal which had undergone surgery on the eighth day was tested for retention of the conditioned anxiety response. The animal was placed in the grillbox for 4 min. During minutes 2 through 4, as in the conditioning procedure, the buzzer was sounded; but no electrical shock accompanied the trial. The animal's behavior with respect to entry into new rectangles and to crouching during the period in which the buzzer sounded was noted. The test was then concluded, and the animal's experimental service terminated. On the thirteenth day, the same procedure was followed for those animals which had undergone surgery on the ninth day, the twelfth day having been a final recovery day for them.

RESULTS AND DISCUSSION

Results in Terms of Crouching

The effects of lobotomy may be indicated first in terms of *S*s' crouching responses.

No animal, in either group, ever crouched before being shocked in the grillbox. On the contrary, *S*s moved freely about the apparatus; at the sound of the buzzer during minutes 2 through 4 on the second day, immediately before their first experience with shock, the animals explored actively. After conditioning to the criterion, every animal was, of course, crouching within the first 15 sec. of the buzzer's sounding, and maintaining the crouch until the sound terminated.

After surgery, the great majority of the control group animals persisted in the conditioned response. Sixteen of them crouched as before; the remaining four did not crouch at all. In sharp contrast, almost all the experimental animals lost their crouching behavior and resumed free motion during the buzzer. Only three of the experimental animals crouched as before; the remaining 17 did not crouch at all. When these data are tested by chi square, computed according to a formula for correlated proportions, with correction for continuity and with 1 *df* (4, p. 90), the value obtained is 11.08. This figure is significant far beyond the .01 level.

Results in Terms of Motility

The mean motility score among all *S*s during the first recording period of the first day was approximately 40 rectangle entries. This score was characteristic of both the experimental and control animals. Both groups showed a decrease in motility scores, to the level of 25 entries, during the second recording period of the first day. During the first period of the second day, when the buzzer sounded for the first time, each group averaged about 50 entries. The animals received their initial shocks at the end of this period, and thereafter the mean motility score fell radically to about three entries per period and remained there until surgery.

The effects of lobotomy upon motility were much the same as its effects upon crouching behavior. The mean motility score among the control animals after surgery was 2.95 entries. The mean score among the experimental animals was 42.55. The former figure is comparable to the averages found immediately before surgery; the latter is much like the general level before conditioning began. This difference between groups is best tested in terms of the corresponding mean difference in motility between paired animals. The latter figure is necessarily 39.60, and it is significantly different from zero well beyond the .01 level.

General Observations and Discussion

The quantitative findings may be supplemented and illuminated by certain qualitative observations.

Generally speaking, the lobotomized rats evinced brief, exaggerated emotional responses to such stimuli as momentary noises or the sight of objects thrust toward them. Superficially, this observation suggests that the effect of the surgery in the present investigation might have been, not to eliminate anxiety, but merely to increase emotionality. This explanation would envisage the lobotomized animals as overresponding to the buzzer *in spite of* a still potent conditioned anxiety (cf. 3). Although this interpretation remains as a logical possibility, the nature of the experimental animals' behavior during the test trials does not favor it. That behavior closely resembled the behavior seen before conditioning ever began: the animal remained relatively quiescent until the buzzer started to sound, and then it embarked upon exploratory activity; this activity was quite deliberate and persistent, however, and there was no manifestation of the conflict and disorganization required by a hypothesis of hyperemotionality. These facts are well mirrored, of course, by the quantitative data already presented.

A second incidental observation was that the experimental animals seemed more debilitated by surgery than did the controls. This difference between the groups constituted something of a conservative factor, inasmuch as it operated to minimize the group differences in motility. Generally speaking, the experimental animals were not at a great disadvantage, but there were exceptions to this generality: two experimental animals blinded themselves during recovery from surgery (by scratching at their sutured incisions), and they subsequently sat immobile during the retention test. It is evident that a recalculation of statistics, not using the data from these animals, would merely enhance the difference between the groups' mean motility scores.

If frontal lobotomy did indeed tend to eliminate anxiety in the present investigation, it undoubtedly did so as part of a more general alteration of response tendencies. What this over-all effect really is constitutes, as is widely recognized, an extremely complicated problem whose discussion lies beyond the scope of this paper.

SUMMARY AND CONCLUSIONS

Twenty experimental and 20 control rats were conditioned to display anxiety (crouching and immobility) in a grillbox. The experimental animals were then subjected to frontal lobotomy, and the control animals to a sham operation. Upon retesting for anxiety, it was discovered that the experimental animals displayed fewer of the responses indicative of anxiety than did the controls; differences were significant well beyond the .01 level of confidence. The common notion that lobotomy proper tends to abolish anxiety thus receives considerable support.

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THE EFFECT OF ELECTROCONVULSIVE SHOCK ON A CONDITIONED EMOTIONAL RESPONSE: A CONTROL FOR ACQUISITION RECENCY

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Previous research has indicated that a series of 21 electroconvulsive shocks (ECS) can have the immediate effect of virtually eliminating a conditioned emotional response (CER) of the "fear" or "anxiety" type in rats (3). This response was established in a Skinner-box situation *after* the animals had acquired a lever-pressing habit for an aperiodic water reward. The CER appeared as a cessation of lever pressing, accompanied by crouching and defecation, during presentation of a clicking noise which had previously preceded shock to the feet. It has been argued that the effects of ECS in these experiments were specific to the CER, since lever pressing in the absence of the clicker survived the treatments apparently unaffected.

Duncan (2), however, has presented evidence suggesting that the effects of ECS are specific to the most recently learned habits. It is possible, therefore, that the differential effects of ECS in the previous experiments (3) may be attributable solely to the fact that the emotional response was acquired more recently than the lever-pressing habit.

The present experiment attempts a critical control for this possibility. With a technique similar to that reported by Libby (4), the CER was conditioned *before* acquisition of the lever-pressing habit. In all other respects, however, the general procedures followed those employed in the previous experiments (3).

METHOD

Subjects

Twenty-four male albino rats 60 to 90 days old at the start of the experiment served as *Ss*.

Emotional Conditioning Procedure

Emotional conditioning trials took place in the Skinner boxes (with the levers inoperative) *before* lever-pressing training began. All animals received 16 emotional conditioning trials. Each trial consisted of a 3-min. presentation of a clicking noise which terminated contiguously with a momentary shock (approximately 1.5 ma.) to the feet, delivered through the grill floor of the apparatus. The emotional conditioning was accomplished on two successive days by administering eight trials per day spaced at random intervals throughout a 2-hr. session.

Lever-Pressing Training

On the day following the final set of emotional conditioning trials, lever-pressing training began, first for a regular and then an aperiodic water reward. The animals then received seven daily 12-min. sessions in the apparatus, without clicker or shock, to stabilize their lever-pressing output. All animals were on a 23-hr. water-deprivation schedule.

Electroconvulsive Shock Procedure

Beginning on the day following the seventh 12-min. lever-pressing session, the animals were divided randomly into an experimental group (12 rats) and a control group (12 rats). The experimental animals received a series of 21 ECS treatments, 3 per day for seven days, while the control animals remained in their home cages. All animals had free access to food and water in the home cages during this seven-day period. The ECS apparatus and procedure were the same as those employed in previous experiments (3). During the treatment period, 3 experimental animals developed flaccid paraplegia and had to be destroyed.

Retention Tests

Following the last ECS, all animals were again placed on the 23-hr. water-deprivation schedule. On the second post-ECS day, they received a 12-min. session in the lever-pressing apparatus without clicker or shock. On the third day following the last ECS, all animals were tested for retention of the conditioned emotional response by a single unreinforced presentation of the clicker alone during the 12-min. lever-pressing session. Following 30 days' rest in the home cages without further lever pressing or clicker presentations, the experimental animals received a second retention test according to the same procedure.

RESULTS AND CONCLUSIONS

During the 12-min. Skinner-box session on the second day after ECS, all animals showed complete retention of the lever-pressing habit. During the post-ECS retention test for the conditioned emotional response on the following day, however, only the control animals stopped pressing the lever and defecated during presentation of the clicker. In contrast, all the nine surviving experimental animals continued to press the lever in the presence of the clicker, and none defecated. The effects of the ECS treatments appear to have been quite specific in virtually eliminating the CER without affecting the more recently acquired lever-pressing habit.

As an additional control for the effectiveness of the clicker-shock pairings, the nine experimental animals were given a second retention test, 30 days after the first one. There were no intervening lever-pressing trials or clicker presentations. Previous experiments (1) have shown that the CER attenuated by ECS tends to reappear within a month following the treatments. The reappearance of a strong conditioned emotional response in all nine experimental animals on this second retention test provides assurance that the CER was present in these animals prior to ECS. Furthermore, this confirms the specific attenuating effect of ECS upon the CER irrespective of acquisition recency.

SUMMARY

The present experiment investigates the role of acquisition recency in the reported differential effects of ECS on a conditioned emotional response (CER) and on a lever-pressing habit. The CER appeared as a depression in the lever-pressing curve. A series of 21 ECS virtually eliminated the emotional response acquired prior to lever pressing, but had no apparent effect upon lever pressing in the absence of the emotional stimulus. It is clear from these results that the differential effects of ECS cannot be attributed solely to differences in acquisition recency.

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THE RELATION BETWEEN FEAR AND EXPLORATORY BEHAVIOR

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The results of a series of experiments by the senior author (5, 6, 7, 8) have provided strong support for the hypothesis that novel stimulation arouses the exploratory drive which leads to exploratory behavior. The experimental findings also show that exploratory behavior is not attributable to the hunger or thirst drive, nor to the general activity drive.

In all these experiments, exploratory behavior has been operationally defined as the locomotor behavior of rats given their first exposures to simple mazes that contain no extrinsic rewards such as food or water. It is possible that this kind of behavior is motivated by fear rather than by the exploratory drive. Hebb (2) has reported that certain forms of novel stimulation arouse fear in the chimpanzee. And various authors, e.g., McDougall (3), have suggested that novel stimulation arouses fear. In other words, it is possible that novel stimulation evokes the fear drive, which produces the systematic type of maze behavior we have termed exploratory behavior.

The present paper is the first of a series concerned with the relation between fear and exploratory behavior. It summarizes the results of three experiments and presents in detail the findings of a fourth. The basic plan of these studies is to induce fear in rats experimentally, and then to determine its effects upon their exploratory behavior in simple mazes. If exploratory behavior is motivated by fear, then it should increase in amount when fear is induced. Further, as the strength of the induced fear increases, the amount of exploratory behavior should also increase.

SUMMARY OF THE FIRST THREE EXPERIMENTS

In the first experiment, each of ten rats was placed in a large metal can, subjected to 30 sec. of stimulation produced by three loud buzzers attached to the can, then placed immediately in an enclosed Y maze and allowed to explore freely for 10 min. Ten control animals received the same treatment except that the buzzer stimulation was omitted. Each rat received two such trials, spaced 24 hr. apart. Records were taken of amount and orderliness of exploratory behavior in the Y maze. The results show no difference between the experimental and control groups in either amount or orderliness of exploratory behavior. During the buzzer stimulation, the experimental animals exhibited signs of fear such as urination and defecation.

In the second experiment, each of seven rats was placed on a large elevated grid floor, subjected to 20 sec. of shock delivered through a 150-v., 250,000-ohm circuit, then placed immediately in the Y maze and allowed to explore freely for 10 min. Seven control animals were given the same treatment except that shock was omitted. Each animal received two such trials, 24 hr. apart. The results show no differences between groups in orderliness of exploratory behavior and only one difference in amount of exploratory behavior: during the first 30 sec. in the maze the experimental animals exhibited a significantly greater amount of activity than the control animals.

In the third experiment, fear was induced in the exploratory situation. A buzzer was attached to the outside of the end of each arm of the Y maze. Three groups of eight rats each were used. Each animal was given one 10-min. period of exploration in the maze. For group E2 the buzzers were sounded for 30 sec. beginning 60 sec. after the start of the exploratory period; for group E6 the buzzers were sounded for 30 sec. beginning 300 sec. after the start of exploration; and for group C the buzzers were never sounded. Records of were taken of amount and orderliness exploratory behavior. No differences in orderliness of exploratory behavior occurred among groups. Figure 1 shows average number of 12-in. maze sections explored as a function of time of exploration. The data for groups C and E6 are combined for the first 5 min., and the data for group E2 are omitted for the last 5 min. These graphs show that after the cessation of the buzzer stimulation, amount of behavior decreased in both experimental groups to a level below that of the

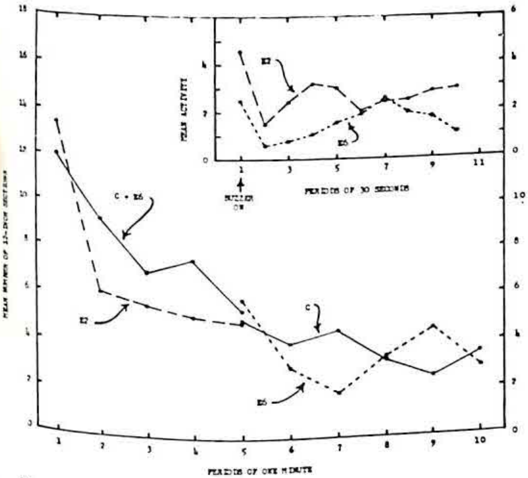

FIG. 1. Average amount of exploratory behavior as a function of time of exposure to the maze. The inset graphs show mean amount of behavior as a function of 30-sec. periods during and after buzzer stimulation: the first point on the graph for group E2 represents mean amount of activity during the 30-sec. period beginning with the sixtieth second of exploration; and the first point for group E6 shows the corresponding value beginning with the three-hundredth second.

control group. The decrease is significant at beyond the .01 level for both experimental groups; and average amount of activity is significantly less for group E2 on minute 2 and for group E6 on minute 7 than for group C on corresponding minutes. The graphs also reveal that the decrement was temporary: amount of exploratory behavior gradually returned to normal over a period of 2 to 4 min. The details of the recovery process may be seen in the inset graphs of Figure 1, which show mean number of 12-in. maze sections traversed per 30-sec. period during the buzzer stimulation and for 4½ min. afterward. The increase from point 2 to point 4 on the inset graph for group E2 and the increase from point 2 to point 7 for group E6 are significant at between the .05 and .02 level. Group C shows none of the above-mentioned changes in amount of exploratory behavior exhibited by the experimental groups. Qualitative observation of the animals indicated that the buzzer stimulation induced at least a mild state of fear.

The results of these three experiments are uniformly negative with respect to the hypothesis that exploratory behavior is motivated by fear. The findings of the first two studies indicate that fear induced outside of a novel situation exerts little if any effect upon exploratory behavior in that situation. The results of the third experiment show that fear induced either early or midway in a period of exploration in a novel environment produces a temporary *decrement* in amount of exploratory behavior. The experiment reported below provides a fourth test of the fear hypothesis. It is designed to determine the effects of strong fear induced in a novel situation upon amount of exploratory behavior in that situation. Fear was aroused by electric shock administered either early or midway in a period of exploration.

EXPERIMENT IV

Method

Subjects. Eighteen female rats of the Wistar strain, about 90 days of age, which had never been used in an experiment, served as *S*s. All rats had free access to both food and water at all times except during the short experimental periods. The animals were thoroughly tamed prior to the experiment.

Apparatus. An enclosed maze was constructed from white Celotex walls 24 in. high placed on a grid floor to form alleys 4 in. wide. The maze was rectangular in shape, measuring 18 by 36 in. along the outside walls, with a central alley bisecting the two long sides of the rectangle. Thus, it consisted of seven alleys, each 14 in. long. The maze was placed in the center of an 8-ft. square enclosure formed by black curtains. Illumination was provided by a single 40-w. shaded bulb suspended 5 ft. from the floor directly over the center of the maze. Electric shock could be delivered to the grid floor of the maze through a 150-v., 250,000-ohm circuit.

Procedure. Prior to the experiment, which lasted three days, six rats were assigned at random to each of three groups, a control and two experimental groups. On each of the three days, each animal was placed at the center of the maze and allowed to explore freely for a period of 10 min. On day 1 and on day 2, the rats in group E2 were given three shocks, totaling 20 sec., during their second minute of exploration; the animals in group E6 were treated similarly during their sixth minute of exploration; and the rats in group C were not shocked. Shock was administered to the experimental animals during these periods of their respective shock minutes: 0 to 5 sec.; 10 to 15 sec.; and 20 to 30 sec. On day 3, no shock was given to any of the groups. The number of 14-in. maze sections traversed per minute was recorded for each animal on each day. The criterion for a maze-section traversal was a full body-length entry, excluding the rat's tail, into one of the seven maze alleys.

Results

The major results are summarized in Figure 2, which shows mean number of 14-in. maze

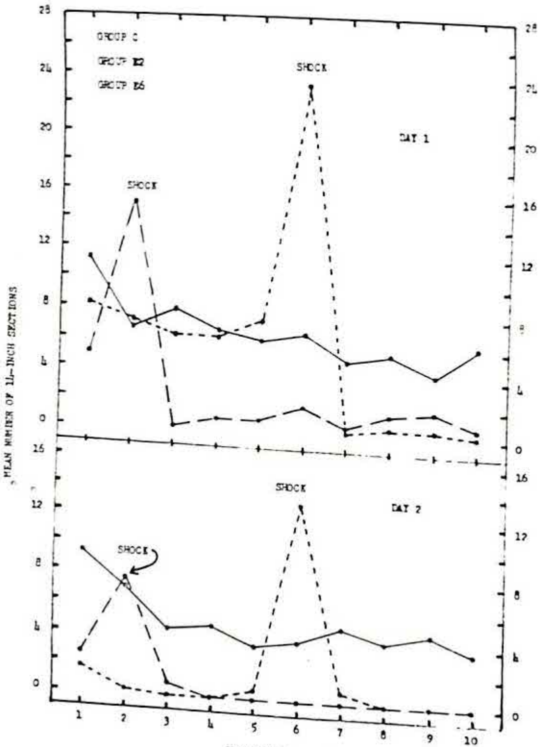

FIG. 2. Average amount of maze activity as a function of time of exposure on day 1 and on day 2.

sections traversed as a function of time of exposure for each group on day 1 and on day 2. On day 1 the curves for the three groups begin at about the same level, and the curve for group C decreases in a fairly regular manner. The curves for groups E2 and E6 show a sharp increase in amount of activity during the shock periods, a sharp decrease to a level well below that of the control group immediately upon the cessation of shock, and a very low level of activity during the remainder of the exploratory period. Statistical analyses bear out these statements. The results of an analysis of variance reveal that the groups do not differ in amount of activity during the first minute (*F* of 3.00; 2 and 15 *df*). The increase and the decrease in amount of behavior are significant at beyond the .001 level for both experimental groups. During the period after shock, mean amount of activity is significantly less (.01 level or beyond) for the experimental groups than for the control group. Also, average amount of activity is significantly greater (.001 level) for the experimental groups during their respective shock periods than for the control group during the corresponding periods.

On day 2 the experimental animals were almost completely inactive except during the shock periods. As on day 1, the increase in amount of behavior during shock and the decrease after shock were highly significant for both groups, and amount of activity after shock was significantly less for both groups than for group C. On day 3, on which no shock was given to any of the groups, the animals in both experimental groups were almost completely inactive, whereas the group C animals exhibited a normal amount of exploratory behavior.

Inspection of Figure 2 reveals that the shock produced a greater amount of activity in group E6 than in group E2. The respective means during the shock periods are 23.5 and 15.1 on day 1, and 13.0 and 7.5 on day 2. The difference between the first pair of means is significant at beyond the .01 level (*t* of 3.23; 10 *df*), and the difference between the second pair is significant at about the .05 level (*t* of 2.21; 10 *df*).

Figure 2 also shows that each experimental group exhibited only about half as much activity on day 2 as on day 1 during the shock period. Mean amount of activity for group E2 during minute 2 is 15.1 on day 1 and 7.5 on day 2. Corresponding means for group E6 on minute 6 are 23.5 and 13.0. The difference between the first pair of means is significant at the .001 level (*t* of 7.72; 5 *df*); and the difference between the second pair is significant at beyond the .01 level (*t* of 4.20; 5 *df*).

Qualitative observation indicated that after their first shock, all the experimental animals exhibited strong fear of the maze, e.g., defecation, urination, and a marked "reluctance" to be placed in it on days 2 and 3.

DISCUSSION

The results of these four experiments may be summarized as follows: (*a*) Neither strong auditory stimulation nor electric shock administered immediately prior to a period of exploration in a simple maze exerts any appreciable effect upon exploratory behavior. (*b*) Auditory stimulation administered during a period of exploration in a maze produces a temporary decrement in amount of exploratory behavior which occurs immediately after the cessation of stimulation. (*c*) Shock administered during a period of exploration in a maze produces (*i*) an above-normal amount of activity during the shock period when given either early or midway in the exploratory period, (*ii*) a significantly greater amount of activity during the shock period when given midway rather than early in the exploratory period, and (*iii*) a significantly smaller amount of activity on the second trial than on the first, whether presented early or midway in the exploratory period. (*d*) Immediately after the cessation of shock administered in a maze, amount of activity drops to a low level which persists for the duration of the exploratory period and which recurs after a 24-hr. rest period.

Although the two kinds of stimulation employed in these experiments differ qualitatively as well as quantitatively, it seems plausible to assume that they are on a continuum with respect to their fear-arousing properties. Qualitative observation indicated that both the buzzer and the shock stimulation evoked fear in the experimental animals, and that the strength of the induced fear was much greater in the case of shock stimulation. If these statements are correct, then all of the experimental findings are negative with respect to the hypothesis that exploratory behavior is motivated by fear. According to this hypothesis, amount of exploratory behavior should increase as the strength of the fear drive increases. The results show that fear induced outside of an exploratory situation exerts little or no effect upon amount of exploratory behavior in that situation, and that fear induced in an exploratory situation produces a *decrement* in amount of exploratory behavior, the magnitude of the decrement increasing with strength of fear. The temporary decrement found in the third experiment indicates that mild induced fear dissipates after the fear-arousing stimulation is removed. This finding is in agreement with data reported by Skinner (9) and Estes (1) showing that mild punishment produces a temporary decrement in rate of operant behavior.

The detailed findings of the fourth experiment require discussion. The high level of activity during shock is interpreted as escape behavior motivated by pain. The very low level of activity after the cessation of shock is explained as follows: It has been established that stimuli associated with pain acquire the power to evoke fear, and that fear leads to avoidance behavior (4). Thus in the present experiment, shock generated a strong conditioned fear which, because the maze was homogeneous with respect to its stimulus properties, generalized to all parts of the maze. Hence, no matter which way an animal turned, the maze stimuli evoked strong avoidance tendencies. On the other hand, novel stimulation such as that provided by a maze normally evokes strong approach tendencies that result in an animal's thoroughly exploring the novel situation. Thus, in the present study the experimental animals were subjected to a double approach-avoidance conflict. Because the strong avoidance tendencies based upon the fear drive predominated over the normal approach tendencies based upon the exploratory drive, a very marked and persisting decrement in amount of exploratory behavior occurred.

The facts that group E6 exhibited more activity during shock than group E2 on both day 1 and day 2, and that both groups were less active during shock on day 2 than on day 1 remain to be explained. Both these results are interpreted in terms of conflict. The results of the present study indicate that shock administered in a novel environment produces escape behavior (for the duration of the shock), thus increasing amount of activity. On the other hand, the findings of this and the third experiment indicate that fear evoked in an exploratory situation produces avoidance tendencies that reduce amount of activity, and that the decrement in amount of activity is a positive function of the strength of the fear drive. Thus, when both shock and fear are present, a conflict occurs. This can be termed an "escape-avoidance" conflict. In the present experiment, intensity of shock was held constant; hence, any variations in amount of activity during shock should reflect variations in the strength of the fear drive. Qualitative observation has repeatedly suggested to the authors that novel stimulation arouses the fear drive (as well as the exploratory drive) and that fear decreases in strength with time of exposure to that stimulation.[1] If this is so, then the strength of the avoidance tendencies evoked by the maze should decrease with time of exploration, resulting in a greater amount of activity during shock for group E6 than for group E2, as was found. And, the strength of the fear drive evoked by the maze should have been greater on day 2 than on day 1 because the shock given on day 1 generated a strong conditioned fear of the maze in both experimental groups; hence, the strength of the avoidance tendencies evoked by the maze was greater on day 2 than on day 1, and the result was a lesser amount of activity during shock on day 2 than on day 1, as was found.

SUMMARY AND CONCLUSIONS

The results of three experiments are summarized and the detailed findings of a fourth are presented. The purpose of these studies is to test the hypothesis that the exploratory behavior of rats in simple mazes is motivated by fear. Fear was induced immediately prior to a period of exploration by auditory stimulation in the first experiment and by electric shock in the second. Fear was induced either early or midway in a period of exploration by auditory stimulation in the third study and by shock in the fourth. Measurements of both amount and orderliness of exploratory behavior were recorded in the first three experiments; measurements of amount of exploratory behavior were taken in the fourth experiment. The results are summarized at the beginning of the preceding section of this paper. The following conclusions are drawn from the findings of these experiments: (*a*) Fear induced immediately prior to a period of exploration in a novel environment exerts little or no effect upon exploratory behavior in that environment. (*b*) Fear induced in a novel situation reduces amount of exploratory behavior in that situation, the magnitude of the decrement increasing with strength of fear. (*c*) The decrease in amount of exploratory behavior produced by induced fear is readily explained in terms of conflict theory. (*d*) The results of Experiment IV provide a basis for postulating a new type of conflict: the "escape-avoidance" conflict. (*e*) Finally, exploratory behavior is not motivated by fear. Rather, it is motivated by the exploratory drive which is evoked by novel stimulation.

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[1] The results of experiments as yet unpublished support the hypothesis that novel stimulation arouses the fear drive as well as the exploratory drive, and that the strength of the former drive decreases with time of exposure to a situation.

PAW PREFERENCE IN CATS RELATED TO HAND PREFERENCE IN ANIMALS AND MAN

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During the last twenty years various workers have turned their attention to the phenomenon of a preference in the use of one or other of the forelimbs or claws in parrots, rats, monkeys, chimpanzees, and man. It is, however, noteworthy that all these *S*s habitually use either the forelimb or claw to convey food to the mouth. Therefore it seems worth while to investigate a mammal that does not normally use its limbs in this way.

Such an animal, in order to be examined for preference in the use of one or other forelimb, needs to have the use of these limbs sufficiently developed to perform a simple test, and to be obtainable in large enough numbers to provide a satisfactory sample. The common cat meets these requirements; therefore we decided to use it in our experiment.

We also wished to compare the incidence of paw preference, if it were found to be present, in the cat, which does not use the forelimbs in normal feeding, with that of other animals that do and which have been studied by other workers.

Then, finally, having collected our data and compared them with previous findings by others and ourselves, we related our inferences to the problem of whether anatomical structure or the psychological environment is the dominant factor in determining handedness.

METHOD

Subjects and Apparatus

Sixty cats, selected at random, were used in this experiment. In marking they were black, black and white, tabby, tortoise-shell, ginger, and many of the possible permutations of these markings; some were long-haired, some short-haired; 27 were male and 33 female. We had no means of ascertaining their age, but their weight varied from 1 kg. to 5.2 **kg**. None was purebred Siamese, nor, as far as we know, of Siamese descent.

The apparatus used consisted of a block of wood, 2 by 9.5 by 28 cm., painted black, and a tube of glass 0.3 cm. thick with an inner diameter of 6.5 cm. and 15 cm. long. This glass tube was placed centrally on the board and held in position by two elastic bands so as to be readily removable for cleaning and to enable the board to be scrubbed.[1]

Procedure

The apparatus was baited by placing a small piece of raw rabbit about 6 cm. from one end of the glass tube so that, in order to obtain it, the cat had to reach in with one or other of its paws. Raw rabbit proved the best bait for it was unrationed, readily obtainable, and universally popular with our *S*s.

The cats were trained to use the apparatus by first being fed with small pieces of rabbit. When the cat was eating greedily, a bait was placed at the opening of the tube where the animal could reach it with its mouth. This procedure was repeated several times. By then the cat was quite familiar with the apparatus, and the bait was placed further into the tube, where it could be reached neither by the mouth nor by the tongue. The next stage of reaching the bait with the paw was the most difficult part of the training. During this period it was noticed that in most cases the cats with a strong preference for one paw learned to obtain the bait more readily than the cats that were ambidextrous.

When the cats were using the apparatus freely, testing was begun. For this the cat was placed on a wooden-topped table 1.8 by 0.6 m. with the walls of the room along one long and one short side. It was left free from all restraint, and the baited apparatus was placed on the table top.

We found in preliminary investigation that if the apparatus was always placed just in front of the cat, it tended to sit down and make the same movement at each trial. In order to avoid this stereotype, the board was presented in a variety of ways, sometimes close to the cat, sometimes the length of the table away, sometimes behind the cat, sometimes in front, sometimes so that the cat had to move toward *E*, sometimes away from him; but in every case *S* was made to move, and in many cases turn its whole body.

One hundred reaches were given, usually on the same day, in two series of 50 with about 15 min. between each series. The number of times each paw was used in each series was recorded separately for all but the first ten cats. The standard adopted in the estimation of paw preference was that used by Tsai and Maurer (9) in their experiment with rats; i.e., an animal was only

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[1] The apparatus has, when modified, proved of value in the study of parietal lobe lesions (GLEES, P., & COLE, J. Comparison of anterior parietal lesions with posterior parietal lesions in trained monkeys. *Rep. Congrès Neurologique International, Lisbonne*, 1953, **2**, 262–267).

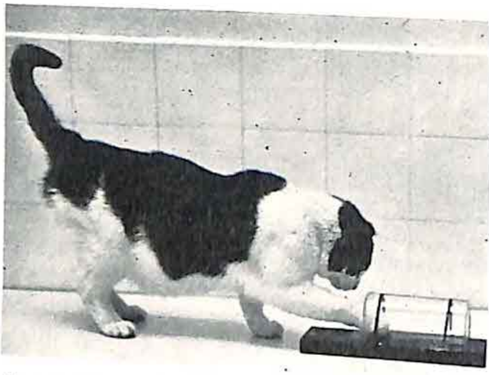

FIG. 1. Cat making a "reach" and obtaining bait from the testing apparatus.

considered to show paw preference if the same paw was used in 75 to 100 per cent of the reaches.

The cats appeared to find the experiment agreeable, in most cases purring loudly with the tail erect and waiting eagerly for the presentation of the apparatus. Figure 1 shows one of our cats using the testing apparatus.

RESULTS

The results of the experiment are shown in Table 1. From this it will be seen that of the 60 cats used, 35 (58 per cent) had a marked preference in the use of one or other paw. Of these, 12 (20 per cent) were right-pawed and 23 (38.3 per cent) left-pawed; the remaining 25 (41.7 per cent) were classed as ambidextrous since they did not use one paw 75 times out of 100 reaches.

Of the 35 cats that had a dominant paw, 13 used the same paw for all 100 reaches, 15 the same paw for 90 to 99 per cent of the reaches, and 7 for 75 to 89 per cent; this would indicate a tendency for paw preference to be very definite when present.

When the two sexes were compared, slightly more females (63.7 per cent) than males (51.9 per cent) were found to have a dominant paw, but the number tested was too small to attach any significance to this difference.

The separate score on each half of the 100 trials, which was kept for 50 cats, was remarkably consistent. Only 3 animals showed a scatter of as much as 7 points. An incidence of such scatter is illustrated in the score of cat 60, which used the right paw 36 times in the first 50 trials and 29 times in the second 50. If we exclude the 12 cats that used only one paw throughout the test, the 38 remaining *S*s had an average scatter as low as 3.5 trials between the first and second halves of the test.

TABLE 1

Number and Percentage of Cats Showing Paw Preferences*

Group	*N*	Right-Pawed	Left-Pawed	Total Paw Dominant	Ambidextrous
Total	60	12 (20)	23 (38.3)	35 (58.3)	25 (41.7)
Males	27	3 (11.1)	11 (40.8)	14 (51.9)	13 (48.1)
Females	33	9 (27.4)	12 (36.3)	21 (63.7)	12 (36.3)

* Figures in parentheses are percentages.

DISCUSSION

These results show that slightly more than half our cats had a definite preference in the use of one or other forepaw, and among those with a dominant paw more used the left than the right.

Unfortunately, the number of cats referred to by Pike and Chappell (8), is too few to enable us to make a comparison of their work with ours. Comparable studies have, however, been made with rats, notably by Tsai and Maurer, who reported that right-handers predominated among their rats, whereas Peterson (5) in his more extensive experiments concludes that right- and left-handedness occur in about an equal number of cases while ambidexterity is less common.

Friedmann and Davis (3), with 20 parrots of 15 different species, reported that 72.2 per cent of their *S*s showed a definite left-handed tendency. However, if, in order to make a comparison, we apply our standards to their figures, we find that 55 per cent of their birds were left-clawed, 5 per cent right-clawed, and 40 per cent ambidextrous. On the other hand, Finch (2), with his 30 chimpanzees, found the incidence of dominant right- or left-handedness approximately equal and a minority of his *S*s ambidextrous. Two years later Yerkes (10), working with the same animals, obtained similar evidence. Cole and Glees (1) reported a parallel finding in their paper on monkeys, which later observation of a greater number of these animals has confirmed.

From all these studies and the accepted right-handedness of man two facts emerge. The first is that in all the species tested a large proportion of the members prefer one forelimb to the other. However, the actual percentage of dominant handers shows considerable variation among species, being lowest and almost identical in cats and parrots and highest in man, with rats, monkeys, and chimpanzees between the two.

The second fact is that throughout the series of species studied there is no consistent preference for the right side or the left. Of those with one side dominant the left-handers seem to predominate among parrots and cats, the right-handers among humans, while rats, monkeys, and chimpanzees seem to be about equally divided in their preference for one or other forelimb.

The hypothesis that hand preference is the result of feeding habits might be advanced in the case of parrots, rats, monkeys, chimpanzees, and man, all of which use a limb in normal feeding to convey food to the mouth, but it is not a satisfactory explanation for paw preference in the cat. Nor does this hypothesis explain why members of the same species should form different habits; much less can it account for the fact that many do not develop any preference at all but remain ambidextrous.

On this point Peterson's (6) conclusion after his experiment on transfers in handedness in the rat from forced practice is relevant: "Methods are effective in producing a greater use of the non-preferred hand. Although there is a trend towards more use as more practice is given, there are pronounced exceptions, indicating that something other than practice is operating to determine the strength of the original preference" (6, p. 189).

What Peterson's "something other" may be is suggested by the experiment of Pike and Chappell with cats, by Peterson and Chaplin (7) with rats, and by our own observations of operated monkeys. In all these cases lesions in the motor areas of the hemisphere contralateral to the preferred hand produced a transfer in the hand used.

Furthermore, as Peterson and Chaplin point out, destruction of under 5 per cent of the fiber paths of the pyramidal system has been shown to produce transfers, so that these authors' conclusion "that the pyramidal systems of the cerebral cortex are the prepotent mechanisms in the control of handedness in the rat" (7, p. 361) would appear to be well established. In complete agreement with Peterson's work is the suggested explanation of handedness put forward by Cole and Glees. While studying pyramidal degeneration in monkeys by means of the Marchi technique after motor cortex lesions, Glees found that a varying number of fibers remained uncrossed. Consequently, one-half of the spinal cord receives a greater assemblage of fibers made up of crossed and uncrossed fibers than the other. It will be remembered that these authors using monkeys found and based their conclusions upon uncrossed fibers in the lateral corticospinal tract (4), as there is little evidence that the monkey has a ventral uncrossed pyramidal tract.

It may well be, therefore, that if and when one hemisphere gives rise to a comparatively large proportion of crossed fibers in either pyramidal tract, the result is the preference of the contralateral forelimb in the performance of motor acts.

It would also follow that in cases where the crossing of fibers is approximately equal, a condition of ambidexterity occurs. This hypothesis offers an explanation of our observations on paw preference in cats, and does not run counter to the results of the experiments of other workers to which we have referred. Furthermore, a similar preponderance of ascending fibers from one or other side occurring in the sensory system might, as suggested (1), exert a considerable influence on the preference in the use of one or other hand or paw.

These suggestions, based on experimental evidence obtained from animals, would apply equally well in the case of man. As is well known, numerous workers approaching our problem as psychologists have listed various possible environmental determinants of hand preference in man. Nevertheless, our conclusions, especially when reinforced by the work of Peterson, would suggest that the explanation of what is called handedness is to be found by anatomical rather than purely psychological investigations.

SUMMARY

Sixty cats were tested for paw preference by being made to reach into a glass tube for food.

If we consider the use of the same paw for 75 per cent of the hundred reaches made as evidence of paw preference, 20 per cent were right-handed, 38.3 per cent left-handed, and 41.7 per cent ambidextrous.

The hypothesis that preference in the use of a hand is the result of feeding habits is examined and rejected.

It is suggested that variation in the number of fibers crossing to form the pyramidal tract in the spinal cord offers an explanation of preference for the use of one or other limb, especially if it is combined with a similar inequality in the ascending sensory system.

It is concluded that innate anatomical structure is probably of greater significance in determining preference in the use of a fore-limb than are environmental psychological factors.[2]

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INTEROCULAR TRANSFER OF LEARNING IN VISUALLY NAIVE AND EXPERIENCED INFANT CHIMPANZEES

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In higher primates some fibers of the optic nerve cross at the chiasma to the contralateral cerebral hemisphere and some remain on the ipsilateral side. The number of crossed and uncrossed fibers is estimated to be about equal in monkey and in man (1), and this probably also holds for chimpanzee. Fibers from the corresponding parts of the two retinas make synapses at the lateral geniculate body, and these fibers terminate together at the striate cortex. The two lateral geniculates have no known interconnections; they probably serve only as relay stations. The existence of direct pathways from one cortical visual area to the other also has yet to be clearly demonstrated. These anatomical considerations suggest that the functional equivalence of the two eyes—i.e., the fact that the world looks the same to us through either eye alone, and that an untrained human adult eye mediates visual tasks learned monocularly through the other eye—probably is not determined solely by innate organization between either the two geniculates or the two striate areas.

Previous studies on interocular transfer of visual habits in various animals indicate the importance of both structural and experiential factors. In species that have crossed optic fibers only, such ability may depend on the establishment of interconnections between the two optic tecta. Sperry and Clark (8) reported that in a teleost fish interocular transfer occurred in some individuals and not in others. Levine (3) found that in pigeons such transfer occurs only when the stimuli are placed in the ventral visual field. Furthermore, pigeons reared in diffused light, and having no experience with visual patterns, failed in immediate transfer of a monocularly learned problem to the contralateral eye. However, there was considerable saving in learning the problem with the second eye (7). Animals that have both crossed and uncrossed optic fibers, such as the rat (2) and cat (5), show complete and immediate interocular transfer if they are reared in a normal environment. Riesen *et al.* (5) reported that cats reared in darkness and then given patterned light to one eye and diffused light to the other, do not immediately transfer visual discriminations learned with the former eye to the latter eye. (By "patterned light" is meant that provided by an ordinary, lighted room environment, including forms, colors, shadings, and movements of the *S* and of objects in the room. "Diffused light" is homogeneous, nearly white light with no contours or movements.) They acquire the habits with the diffused-light eye, however, with a large amount of saving. This suggests that, in spite of the anatomical convergence of the optic fibers from two retinas to the same visual area, complete functional equivalence of the two eyes is not assured without some patterned-light experience. One uncontrolled factor in the last study is the possibility that some structural changes may occur in the diffused-light eye and may be responsible for the failure of transfer.

The present study was undertaken to determine the occurrence of interocular transfer of visual habits in infant chimpanzees reared under varying conditions of light stimulation: (*a*) monocular light stimulation, one eye with patterned light, the other eye with diffused light only; (*b*) monocular patterned-light stimulation; (*c*) binocular patterned-light stimulation. After visual discrimination habits were learned with one eye, the ability to perform these habits with the other eye was tested.

The results obtained elucidate the role of early visual experiences for the perceptual equivalence of the two eyes in a higher primate having an anatomical basis for binocular fusion.

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METHOD

Subjects

Six infant chimpanzees born at the Yerkes Laboratories were used. They were separated from their mothers within 28 hr. after birth and were reared in the nursery under standard conditions of diet and care.

Experimental and Control Conditions

Experimental condition. Three *Ss*: Laru, female; gestation period, 230 days; birth weight, 1.85 kg. Sally, female; gestation period, 235 days; birth weight, 1.99 kg. Norma, female; gestation period, 239 days; birth weight, 1.83 kg.

Within ten days after birth these animals were placed in a darkroom, with no light stimulation whatsoever, and remained there until age 6 weeks. Thereafter, and until the end of the study, they were given monocular light stimulation, 1.5 hr. daily to each eye, spending the rest of the day in the darkroom. The right eye was given patterned-light experience, as provided by the normal nursery environment. The left eye was exposed only to diffuse, homogeneous, or unpatterned light. Starting at about age 16 weeks, the *Ss* were given monocular training (in two daily 15-min. sessions) on two or more visual discrimination habits, only one or the other eye being uncovered during training on a given habit. After mastery of a discrimination habit with one eye exposed, transfer of this learning with the other eye exposed was tested. If immediate transfer did not occur, the habit was retrained with the second eye. Figure 1 shows eye exposure, training, and testing schedules for all animals.

Control condition I. One *S*: Margo, female; gestation period, 236 days; birth weight, 1.67 kg. This animal was kept in continuous darkness until age 12 weeks. Monocular patterned-light stimulation, ½-hr. daily to each eye was given to age 22 weeks. Thereafter and until the end of the experiment the monocular exposure of each eye to patterned light was 1.5 hr. daily. As with the experimental *Ss*, Margo was kept in the darkroom except during the light exposure, training, and testing periods. Discrimination training was begun at age 22 weeks. Details of the schedule are shown in Figure 1.

Control condition II. Two *Ss*: Malcom, male; gestation period, 226 days; birth weight, 1.94 kg. Neal, male; gestation period, 239 days; birth weight, 2.14 kg. Both *Ss* were reared in the nursery under standard conditions and had normal binocular experience. During training on a visual discrimination habit, however, only the right eye was exposed. In the transfer tests, only the left eye was uncovered (Fig. 1).

Methods of Restricting Light Exposure

Monocular exposure during periods *B*, *C*, and *D* (Fig. 1) was achieved by placing an appropriately shaped piece of adhesive tape over the eye socket, using additional smaller pieces of tape to seal off the edges. Hairs on the orbital ridge were trimmed periodically. Except on very rare occasions the tape adhered snugly to the skin during the 1.5-hr. exposure period or 15-min. training session. During the 1.5-hr. periods of exposure to patterned light, cardboard mailing tubes were usually secured over the arms, so that the animal could not tear off the eye patch with its fingers. The adhesive tape caused no unfavorable effects to the eyelid or skin around the eyeball in any *S*. The animals moved around, wearing the eye patch, without any apparent discomfort.

The method of exposing one eye to diffuse light was similar to that employed in a previous study (4). Adhesive tape covered the right eye. The *S* was secured on a holding board in supine position, facing directly upwards. A translucent hemisphere of Plexiglas (white translucent,—334–2000, .125 in. thick) with an opening for the neck covered the *S*'s head. Five 200-w. bulbs provided indirect lighting in the room. The light seen through the dome is quite homogeneous, showing no lines, contours, or other patterning. It should be noted that when the diffused-light eye was being trained on a discrimination, the infant was neither strapped in this apparatus nor covered by the plastic dome. The diffused-light eye therefore had some patterned-light experience during the training and testing sessions, which is not indicated in Figure 1.

The two 1.5-hr. periods of either patterned- or diffused-light exposure were given successively every forenoon with only occasional omissions.

Testing Apparatus and Procedures

The method of formal discrimination training was adopted from a previous study (4). The *S* was seated at a feeding table. The *E* raised either the positive or the negative stimulus plaque directly in front of and about 1.5 ft. from the *S*'s face in a predetermined, balanced order. The plaque was held in position for about 5 sec. Correct responses consisted of approaching the positive stimulus or avoiding the negative one. Incorrect responses were approaches to the negative or avoidance of the positive stimulus. A correct approach was rewarded by allowing *S* to drink 1 or 2 oz. of the usual diet—a mixture of milk, Pablum, and a strained vegetable—from a nursing bottle. An incorrect approach was punished by electric shock; *E* touched the *S*'s mouth region with an electrode at the end of a rod. The other electrode from an inductorium having previously been attached to the upper thigh, this produced an unpleasant but not severe shock. For correct avoidance, *E* patted *S*'s head lightly with his finger. If the animal incorrectly avoided the positive stimulus, there was a delay; *E* waited until *S* looked at the plaque and then allowed it to drink an ounce or two. The manner of expressing approach or avoidance varied somewhat among individual *Ss*. The most frequent expression of the former was bringing the head forward, opening the mouth, and making food barks. Avoidance was shown by turning the head away, or covering the head with arms and hands.

The two *Ss* of control condition II needed a fairly long adaptation period in order to accustom them to the eye patches. The other four *Ss* needed only a few preliminary feedings at the table to accustom them to the training routine.

Two training sessions of about 15 min. each were

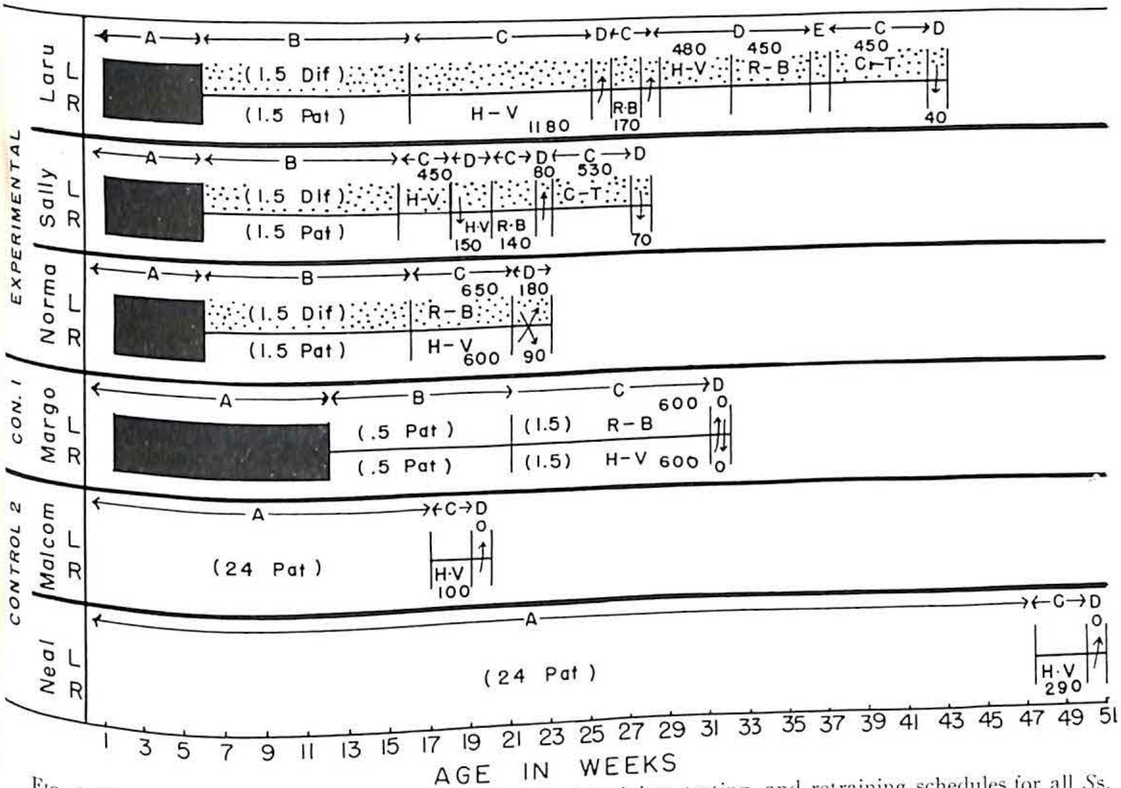

FIG. 1. Summary representation of light conditions and training, testing, and retraining schedules for all *Ss*.

L and *R:* left and right eyes; a line separating these indicates differing light conditions for the two eyes.

A: light conditions during early rearing.

B: monocular light-exposure period.

C: initial training with one eye.

D: interocular transfer tests and retraining with second eye.

E: retention tests of H-V and R-B habits with right eye. Scores were over 90 per cent correct in both cases.

Solid black: total darkness.

Stippled: daily exposure to diffused light (Dif) for hours indicated in parentheses.

Unshaded: daily exposure to patterned light (Pat) for hours indicated in parentheses; except for these periods of monocular light exposure, Laru, Sally, Norma, and Margo were kept in darkness for the duration of the study.

H-V: horizontal (positive) vs. vertical (negative) striations.

R-B: red (positive) vs. blue (negative).

C-T: circle (positive) vs. triangle (negative).

Arrows show direction of interocular transfer tests.

Figures indicate number of trials required for learning (*C*) or for relearning with second eye (*D*). A zero means perfect transfer.

given daily around 10 A.M. and 4 P.M. Each session consisted of 10 trials. The criterion of mastery was 90 per cent correct responses in five successive sessions (50 trials). During the period of training, the *Ss* received most of their nourishment in the form of rewards. Additional milk or fruit juice was fed to them at noon.

After *S* had learned a problem with one eye, transfer tests of this habit were immediately given to the second, untrained eye. During the period of transfer testing, the same discrimination problem was given to the originally trained eye and to the untrained eye. Each eye was tested in one daily session, either in the morning or in the afternoon, according to a prearranged, balanced order. A transfer test required five days (50 trials for each eye). For Margo and Norma, who learned two problems concurrently with different eyes (see Fig. 1), the transfer tests lasted ten days; each problem was given on alternate days. The procedures used in the transfer tests (and in training the second eye) were in all respects similar to those obtaining during original training.

Three discrimination problems were used. (*a*) Horizontal (positive) versus vertical (negative) striations: parallel black and yellow stripes, 2 in. wide, painted alternately on a round plywood plaque (16 in. in diameter). The plaque was presented with the stripes either in horizontal or in vertical position. (*b*) Red square (positive) versus blue square (negative): two plywood squares, 5.5 by 5.5 in., one painted red and the other blue. To the human eye, these colors are approximately equal in brightness. (*c*) Circle (positive) versus triangle (negative): a circle 6 in. in diameter and an isosceles triangle with a 6.5-in. base and 6-in. sides, both cut out of plywood and painted white, with a 0.5-in.-wide black margin around the edges. A handle was fastened to the back of each stimulus for presenting it to the *Ss*.

TABLE 1
Discrimination Learning Results*

Subject	Condition	Habit	(*a*)	(*b*)	(*c*)	(*d*)
Laru	Experimental	H-V	92	90	48	59
		R-B	94	92	60	−165
		C-T	92	94	70	91
Sally	Experimental	H-V	94	94	56	67
		R-B	90	96	56	43
		C-T	92	90	52	87
Norma	Experimental	H-V	90	96	60	70
		R-B	94	92	68	86
Margo	Control I	H-V	96	98	90	—
		R-B	100	100	94	—
Malcom	Control II	H-V	94	94	96	—
Neal	Control II	H-V	94	100	98	—

* Percentage of correct responses (*a*) in 50 criterion trials and (*b*) in 50 test trials with the initially trained eye; and (*c*) in 50 interocular transfer test trials with the second eye. Last column (*d*) shows percentage saving in relearning habit with second eye (when transfer test score was less than 90 per cent).
H-V, horizontal versus vertical striations.
R-B, red versus blue squares.
C-T, circle versus triangle.

Visual Development

Observations of the visual status of the experimental *S*s in daylight were made to obtain some indication of their visual development. Although these observations were not followed systematically, they provide a basis for comparing experimental and normal infants.

In addition, the appearance of the eyes of two experimental *S*s (Sally, Norma) and one control *S* (Margo) was observed in darkness (using infrared rays) by means of a "snooperscope" or "sniperscope." Special effort was made to detect any nystagmus, strabismus, or incoordinated binocular movements. We wish to thank Dr. K. J. Hayes for adapting the snooperscope.

Ophthalmoscopic Examination of the Retinas

For the purpose of detecting any peripheral damage that might have been caused by the restricted light exposures, the retinas of two control (Neal and Margo) and the three experimental *S*s (Laru, Sally, and Norma) were studied with an ophthalmoscope. The *S*s were anesthetized with Nembutal and their pupils dilated by atropine. We are greatly indebted to Dr. Wm. J. Knauer, Jacksonville, Florida, who made these examinations and provided his expert diagnoses.

RESULTS

Training, transfer test, and retraining scores (with the second eye) are shown, in terms of trials before criterion, in Figure 1. Table 1 shows percentage of correct responses with the originally trained eye (both the 50 criterion and the 50 interpolated test trials) and with the second eye; the last column shows percentage savings in relearning the habit with the second eye when perfect transfer was not obtained. (By immediate or perfect interocular transfer is meant that 90 per cent or more correct responses were made by the untrained eye in the 50 trials of the transfer test. More than five errors in the first 50 trials is interpreted as failure of immediate transfer. Degrees of transfer refer to the percentage savings when the previously untrained eye was used in relearning a discrimination previously acquired with the other eye.)

Original Learning and Interocular Transfer of Visual Discriminations

Experimental condition: Monocular diffused-light and patterned-light stimulation. Laru learned two problems with her patterned-light (right) eye. She failed to transfer these habits immediately to the other, untrained eye. Her diffused-light (left) eye made only chance scores (48 per cent and 60 per cent, respectively) in the 50 test trials on each of the discriminations. However, the untrained eye showed a 59 per cent saving in relearning the horizontal versus vertical striations. The fact that more trials were required to relearn the red versus blue squares than had been necessary for original learning may have been caused by the sudden change of *E*s during the course of training, which visibly disturbed the *S*. She learned the third problem, circle versus triangle, in 450 trials with her diffused-light eye. By that time this eye had had about 23 hr. of patterned visual experiences also, during training on the first two problems (about 15 min. per session). When tested for interocular transfer, the untrained, patterned-light eye made 70 per cent correct responses in the first 50 trials. This score is significantly better than chance (at the .01 level) but also significantly inferior (at the .02 level) to the 94 per cent correct responses made by the trained eye (Table 1). Forty additional trials were required to reach the criterion on this third test.

Sally learned the first and third problems with her diffused-light eye, the second problem with her patterned-light eye. In the transfer tests, given immediately following the criterion trials of each discrimination, she failed to show immediate transfer (56 per cent, 56 per cent, and 52 per cent) in the first 50 trials on each of the three problems when tested with the other, untrained eye, no matter which eye was trained first. She showed considerable savings, however, in relearning the problems with the second eye.

Norma learned the horizontal versus vertical striations with her patterned-light eye and the red versus blue squares with her diffused-light eye, concurrently. Scores on the 50 interocular transfer trials with the untrained eye were 60 per cent correct on the former and 68 per cent correct on the latter. Only the second score is significantly better than chance at the .02 level, but it is also significantly inferior (.02 level) to the 92 per cent correct responses obtained with the originally trained eye. By the time of the second transfer test, her diffused-light eye had had about 16 hr. of patterned-light stimulation in daily training sessions. Savings in relearning the H-V habit was 70 per cent; in relearning the R-B habit, 86 per cent.

Control condition I: Monocular patterned-light stimulation. Margo learned the horizontal versus vertical striations with her right eye and the red versus blue squares with her left eye, concurrently. She reached the criterion on the two problems in the same number of trials (600 each), and showed perfect interocular transfer of these habits (Fig. 1 and Table 1). Since Margo had only monocular patterned-light stimulation (to both eyes, separately), these results indicate that binocular visual experience is not necessary for achieving the functional equivalence of the two eyes.

Control condition II: Normal, binocular patterned light. Both animals learned the horizontal versus vertical striations monocularly at a faster rate than did any other *S*. They showed immediate interocular transfer of this habit. The untrained left eye made better than 90 per cent correct responses in the 50 test trials.

It is evident that chimpanzees reared under the experimental condition (one eye exposed to patterned light, the other one to diffused light), in sharp contrast to both control groups failed to show perfect interocular transfer of visual habits learned initially with either eye. It should be noted, however, that even though the eye that was not trained on a particular discrimination failed to show immediate transfer, there were large savings in relearning the problem with the second eye. Moreover, the course of relearning with the untrained eye simulates the original learning, resulting in a gradually increased accuracy of performance. An example of the learning curves is given in Figure 2, which shows Sally's original learning, lack of immediate transfer, and relearning.

Visual Development

Several aspects of the *S*s' visual characteristics were noted occasionally. The main results are summarized in Table 2, together with normative data (provided by Dr. A. H. Riesen). The most striking finding was the occurrence of nystagmus in all *S*s except the two normal controls. Nystagmus was never observed in normally reared infants. The diffused-light eye of the three experimental *S*s showed the most severe nystagmus. It occurred the very first time that eye alone was exposed to patterned light. (Because of technical difficulty, presence of nystagmus in diffuse or homogeneous light was not examined.) In three *S*s (Margo, Laru, Norma) nystagmus of the patterned-light eye did not appear at first but developed gradually and to a lesser degree. Nystagmus of the patterned-light eye of the fourth *S* (Sally) was never observed. Independence of the two eyes with respect to the occurrence of nystagmus is therefore indicated, since it appeared in the diffused-light eye but not in the patterned-light eye of the same infant. The cover nystagmus was characterized by a steady drift toward the nasal and a series of jerky movements toward the temporal side. When both eyes were open, only slight tremors were observed in Margo; and in Laru, Sally, and Norma, nystagmus was less severe then than when only one eye was open. The fast drift of the binocular nystagmus was predominately toward the side of the diffused-light eye.

Laru, Sally, Norma, and Margo were retarded in acquiring the ability to follow a moving milk bottle or a yellow pencil visually. Similarly, they were slower than normals in the development of blinking responses toward a hand quickly moved across or toward their faces.

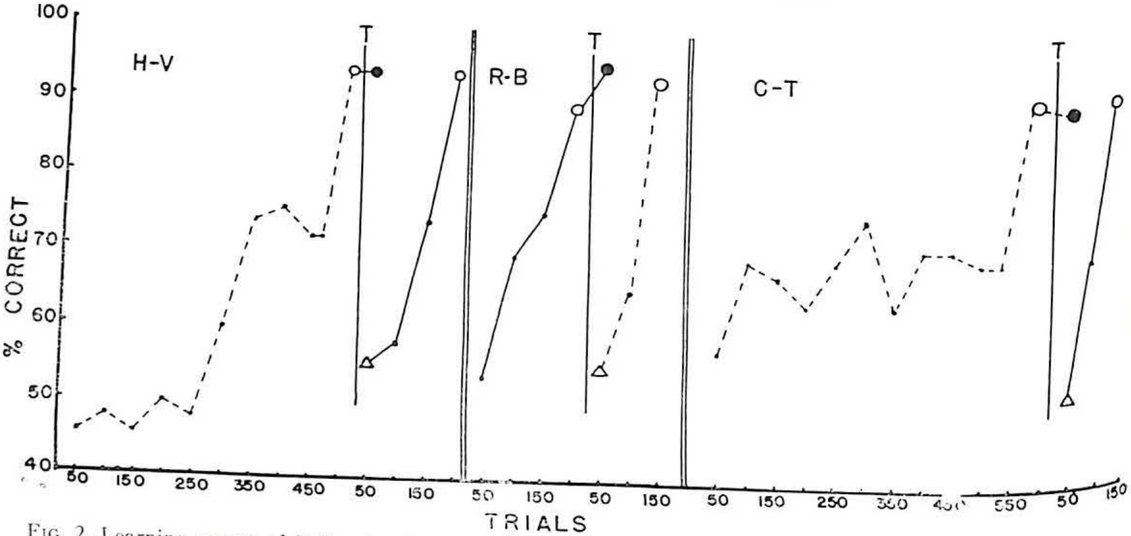

FIG. 2. Learning curves of Sally, showing original learning of the three successive discriminations, the lack of immediate interocular transfer, and relearning with the second eye. Solid line, patterned-light eye; interrupted line, diffused-light eye; open circle, 50 criterion trials; solid circle, 50 trials given to the original eye during the transfer test; open triangle, first 50 trials with the untrained eye (interocular transfer test). The vertical lines labeled with a *T* indicate the beginning of the transfer tests; double vertical lines separate the three discriminations. H-V, horizontal versus vertical striations; R-B, red versus blue squares; C-T, circle versus triangle.

Two other items are not included in Table 1: First, all four *S*s having only monocular visual experience failed to converge to a near object 6 to 8 in. in front of the nose. (In chimpanzees with binocular experience, Riesen observed convergence to 5 in. at 11 weeks, to 3 in. at from 15 to 26 weeks.) Second, three of them (Sally excepted) developed strabismus after they were kept in a patterned-light environment. All symptoms reported above gradually receded after the animals had been kept in the normal nursery environment for various lengths of time following the end of the study.

Results of snooperscope examinations of Sally, Norma, and Margo showed normal appearance and binocularly coordinated movements of the eyes in total darkness. There was no detectable nystagmus or strabismus. It is evident that the visual anomalies cited above were specific to light stimulation.

Ophthalmoscopic Examination of the Retinas

Results of ophthalmoscopic examinations indicated that five *S*s (Malcom was not examined) had normal retinal blood vessels and funduses. The normal control (Neal), examined at the age of 16 weeks, also showed normal appearance of the nerve heads. Margo, Sally, and Norma, examined at age 36 weeks, showed a slight paleness of both nerve heads. Laru, examined at age 30 weeks, showed such paleness only in the left retina.

DISCUSSION

The present study demonstrates a failure of immediate and complete interocular transfer of visual habits in infant chimpanzees reared with one eye exposed to patterned light and the other to diffused light. Two normal controls and one *S* with monocular patterned-light stimulation of both eyes, on the other hand, showed immediate transfer of visual tasks from the trained eye to the untrained eye. This result agrees with previous studies on pigeons (7) and cats (5). Failure of immediate interocular transfer was reported in those animals reared either with both eyes (pigeon) or with one eye (cat) under diffused-light stimulation. Thus, in both lower animals and in a higher primate, development of functional equivalence of the two eyes requires patterned-light stimulation of both eyes.

Evidence was obtained indicating that peripheral factors do not account for the lack of immediate transfer. First, the occurrence of various visual anomalies (nystagmus, strabismus, retardation in blinking reflex and in following objects) were not correlated with

TABLE 2

Observed Occurrences of Nystagmus, Visual Pursuit, Blinking with Movement Across (a) and Toward (t) the Line of Regard

Age in weeks		Subjects												
		Laru			Sally			Norma			Margo			Con-trol*
		R	L	B	R	L	B	R	L	B	R	L	B	B
7	Nystagmus	−						−	+					−
	Pursuit	−						−	−					+
	Blinking a	−						−	−					−
	Blinking t	−						−	−					−
12 to 15	Nystagmus	−			−	++		−	++		−	−		−
	Pursuit	+			+	−		+	−		−	−		++
	Blinking a	−			−	−		+	−		−	−		++
	Blinking t	−			−	−		−	−		−	−		+
22 to 25	Nystagmus	−	++	+	−	++		+	++	+	+	+	?	−
	Pursuit	+	−	+	++	−		++	+	++	+	+	+	++
	Blinking a	−	−	−	+	+		+	+	+	−	−	+	±
	Blinking t	−	−	−	+	−		+	+	+	−	−	−	++
29 to 32	Nystagmus	−	++		−	++	+				++	++	?	−
	Pursuit	++	+		++	+	++				++	++	++	++
	Blinking a	+	+		+	+	+				+	+	+	±
	Blinking t	+	−		++	−	++				++	++	++	++
42	Nystagmus	+	++	+										
	Pursuit	++	++	++										
	Blinking a	+	+	+										
	Blinking t	++	++	++										

R, right eye; L, left eye; B, both eyes.

−, absence; +, slight or variable; ++, severe and consistent occurrence.

?, tremor of the eyeball.

Blank, no observation made.

* These data, from five infants with binocular visual experience, were kindly supplied to us by A. H. Riesen (published in part in reference 4). Blinking to movement across the line of regard normally disappears with age, and was absent in one control at 22 to 25 weeks and 29 to 32 weeks.

the failure of immediate interocular transfer. Margo (control condition I) had as severe monocular nystagmus and retarded general visual development as the three experimental *S*s (see Table 2), yet she showed immediate transfer. Sally had no nystagmus and only slight symptoms in her right eye, but this eye showed the same lack of transfer as the other, more severely affected left eye. The severity of visual anomalies in Laru reached the maximum at the time of her last problem, on which she showed the highest degree of transfer.

Second, in agreement with previous reports on chimpanzees (4) and pigeons (6), the four *S*s with restricted light experience showed a slower rate of initial learning than the normal controls. They also had slightly paler nerve heads in the retinas. For the same reasons discussed above, both the retarded learning and the retinal changes cannot be held responsible for failure of immediate interocular transfer.

The present results also render improbable two other possibilities of accounting for the failure of immediate transfer, namely, that the untrained eye may have been "confused" and not adapted to the transfer test routine, or that *S* may have had no adequate visuomotor associations through the untrained eye to respond correctly during transfer testing, even though the discriminanda themselves may have been recognized. The testing schedule and results of the three experimental *S*s (Fig. 1) fail to support these interpretations. No immediate interocular transfer occurred in these infants no matter whether the problem was trained to the patterned-light eye and tested on the diffused-light eye or vice versa. Sally's performance on her third problem is especially noteworthy. She had had previous experiences on two discriminations (one learned by each eye, monocularly), indicating that she had thoroughly adapted to the testing situation and had made adequate visuo-motor associations to respond appropriately; yet she still made chance scores on the third interocular transfer test.

From these considerations it may be concluded that the lack of immediate interocular transfer in Laru, Sally, and Norma probably is not attributable to peripheral factors, but was caused by mechanisms involving the central nervous system of vision. The convergence of the optic fibers from both retinas to the same cortical areas apparently does not automatically determine the perceptual equivalence of the two eyes. At least initially, some visual experiences obtained through patterned-light stimulation to each eye are necessary to establish such equivalence.

Some of the possible properties of the central mechanisms involved are suggested by a further finding. It is consistent with results reported for pigeons and cats that the untrained eye of the three *S*s showed, not perfect transfer, but considerable savings in relearning. This partial transfer may be a function of partially interconnected neuronal groups in the cortical visual areas. There may be two neuronal groups in each visual area, one group receiving the crossed optic fibers, the other one the uncrossed fibers from the two retinas. These two groups are initially partly overlapping, interconnected, or in part identical. The remaining unconnected neurons are the structural reason for failure of immediate interocular transfer. These neurons may be brought into interrelationship, as in the case of Margo, by receiving monocular patterned stimulation through each eye separately. But unstructured, homogeneous light stimulation is not effective. Once this partial isolation is overcome, the two complete neuronal groups, one for each retina, become equivalent or become a single functional unit. The developmental process of functional equivalence of the two eyes requires patterned-light stimulation to complete a structural overlap of neural substrates for the afferent impulses from the two eyes. Further speculations on the theoretical implications of the present findings must be deferred. It is clear that these results may be readily subsumed under Hebb's schema of cell assemblies and phase sequences. They also are not in any essential way contradictory to Lashley's hypothesis of cortical equipotentiality.

SUMMARY

Six newborn chimpanzees were reared under three conditions of light stimulation. Two controls had normal, binocular patterned-light experience. One *S* (Margo) was kept in total darkness except that one eye at a time was exposed to patterned light, each for 1.5 hr. per day. The three experimental *S*s (Laru, Sally, and Norma) were also kept in total darkness, but one eye was exposed to patterned light, the other to diffused light, each for 1.5 hr. per day. All infants were trained on visual discrimination problems with one eye and were tested for interocular transfer to the other eye.

1. The two normal controls learned to discriminate horizontal versus vertical striations with the right eye and showed immediate interocular transfer of this habit to the left eye.

2. Margo learned the horizontal versus vertical striations with one eye and a red versus blue habit with the other eye concurrently. She showed perfect interocular transfer of both habits.

3. Laru and Sally were trained on three discriminations in succession. Laru learned the first two habits with her patterned-light eye and the third habit with her diffused-light eye. Sally learned the first and third habits with the diffused-light eye, the second habit with the patterned-light eye. Norma was trained on two problems, each to one eye, concurrently. These animals showed no immediate interocular transfer on any of the habits, but relearned them with much saving.

The lack of immediate interocular transfer in the last three *S*s is attributed to a central mechanism rather than to peripheral factors. It is suggested that the functional equivalence of the two eyes in infant chimpanzees is not determined by the structure of the central

visual system alone. The anatomical overlap of optic fibers from the two retinas to the same cortical areas is initially incomplete and not adequate for interocular transfer. Some patterned-light experiences, either binocular or monocular, are needed to achieve complete functional interocular equivalence.

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THE AROUSAL AND SATIATION OF PERCEPTUAL CURIOSITY IN THE RAT

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More and more psychologists have recently been turning to a certain set of related and hitherto neglected phenomena. These include curiosity and exploratory behavior in infrahuman animals (2, 8, 14, 15, 18, 21), curiosity in the human being (4, 5, 6), manipulatory drives (10, 23) and attention to change (3, 7, 9). They undoubtedly merit the increasing attention that is likely to come their way, both because they may throw light on important factors in complex human motivation and because they seem to involve drives which differ in at least two interesting ways from those that have been most intensively investigated to date. For one thing, these drives are manifested by "stimulus hunger" rather than by avoidance of stimulation. Secondly, they depend on appropriate external determinants more than on the internal state of the organism, and yet they do not seem to become attached to cues by learning in the same way as acquired fear or anger.

In a paper published a few years ago (2), the writer offered a theory of curiosity arising out of an experiment with rats. The drive in question may be called "perceptual curiosity" to distinguish it from the "epistemic curiosity" that is more characteristic of human beings (5). Two postulates underlie the theory: (*a*) *when a novel stimulus affects an organism's receptors, there will occur a drive-producing response (curiosity)*, and (*b*) *as a curiosity-arousing stimulus continues to affect an organism's receptors, curiosity will diminish.* As was stated at the time, the provisional form of these postulates leaves some essential questions unanswered. The curiosity drive is said to be aroused by "novel" stimuli, but the word "novel" can have several meanings. Must the stimulus be completely (absolutely) novel, i.e., must it be something the organism has never encountered before, or is it a matter of relative novelty or change, i.e., must the stimulus be novel with respect to what has immediately preceded it or to what has preceded it in the same context? How different must it be from similar stimuli that are familiar? Must its elements be new, or can it be a new combination of familiar elements?

Other problems are raised by the gradual decline in exploratory activity with time. If we are to follow out the implications of Hullian behavior theory, we cannot dismiss this decline glibly as nothing but extinction of exploratory responses. A response should extinguish only if it ceases to be reinforced, and without satiation of the curiosity drive it is difficult to see why this should occur. If, however, we assume that the curiosity drive aroused by a particular object diminishes by being satiated, then the decline in exploration is predictable. A decrease in drive level will first of all mean a decrease in the reaction potentials of exploratory responses (11, 12), and then finally, when there is no drive left to be reduced, the responses will extinguish because they are no longer followed by drive reduction.

Our theory (2) hypothesized that the diminution of curiosity follows a course deducible from Hull's two-factor theory of inhibition, i.e., there should be a rapid but temporary decline in exploration within a single trial (corresponding to I_R), and in addition there should be a more slowly developing permanent decline (corresponding to $_sI_R$). Montgomery (16) found complete recovery of exploratory activity after a 24-hr. rest and concluded that Hull's concepts are not applicable. But it is difficult to accept this argument against the usefulness, as distinct from the complete adequacy, of Hull's formulation. The latter is quite compatible with the possibility that conditioned inhibition ($_sI_R$) might have a subliminal value in certain situations, although the present state of Hull's system, unfortunately, leaves us to ascertain which. Even in motor learning, Kimble (13) found that $_sI_R$ appears only when enough reactive inhibition (I_R) has accumulated to induce a resting response. It seems not unlikely that a permanent decrease in the curiosity aroused by an object will appear only in certain conditions, e.g., when the amount of curiosity reduction through exploration exceeds a threshold value. Be that as it may, one can hardly deny that more study of the temporal course of the decline and recovery of exploration is called for.

The present paper reports three experiments that provide some fresh evidence, but not definitive conclusions, on these points. The experiments also supplement previous studies in another way. Most investigations of exploratory behavior in the rat (e.g., 14, 15, 18, 21, 26) have used the amount of perambulation through maze alleys as the dependent variable. These investigations have yielded many valuable findings, but running through an alley can be motivated by so many different drives and influenced by so many well-known factors that it seems rather an indirect way of revealing what we have called curiosity. Furthermore, whether more running necessarily means more curiosity than less running is a difficult question. Which animal is showing a greater exploratory tendency, one that explores a large number of objects or areas in a short time or one that spends a long time on a few and so remains relatively stationary? It would thus seem desirable to study some form of behavior that is more closely and exclusively tied to curiosity, and approaching and sniffing are likely to fulfill this requirement most satisfactorily for the rat. It would also seem desirable to examine a rat's approaches to particular items of his environment rather than the exploration evoked by the environment as a whole. In the experiments to be reported, as in the earlier study by the same author (2), such a technique was used.

APPARATUS AND SUBJECTS

The *pre-exposure* box was simply a rectangular box, 11 in. long, 4 in. wide, and 6 in. high, with a wire-netting lid.

The *exploration box* (see Fig. 1) was also rectangular, but it was $15\frac{1}{2}$ in. long, 8 in. wide, and 10 in. high. It was covered with a ground-glass lid, so that light entered, but an animal inside it could neither be seen nor see anything outside the box. The two corners at one end of the box were cut off by convexly curved pieces of metal, forming a small alcove in which objects could be fastened. A beam of infrared light passed through the box just in front of the alcove and then impinged on a photoelectric cell. (A Lamphouse Type MLH and an Osram Photoelectric Relay Amplifier Type MD, supplied by General Electric Company, Ltd., London, were used). In circuit with the cell were a stop clock and an automatic counter, so that whenever a rat broke the beam, the counter registered one approach, and the duration of the interruption was recorded to the nearest quarter-second on the clock.

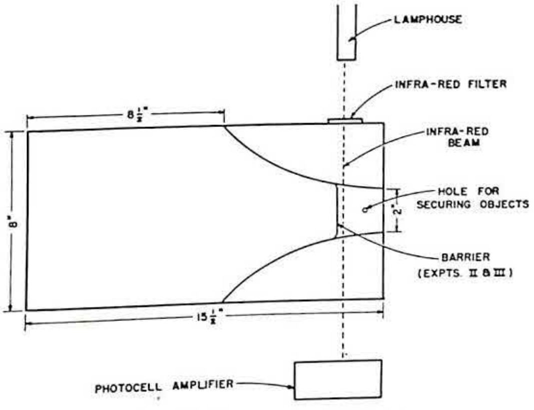

FIG. 1. The exploration box.

After trial 1 of Experiment I, a small screw $\frac{1}{4}$ in. high projected from the floor just behind the beam. This was to discourage sitting in the alcove, but it did not appear to prevent it altogether. For Experiments II and III, the screw was removed, and a narrow strip of metal, painted gray, spanned the alcove of the exploration box just in front of the beam (see Fig. 1). It projected just $\frac{3}{8}$ in. above the floor, and its purpose was to act as a barrier, preventing sitting down in the alcove or backward movement into it, but not interfering with forward exploratory approaches.

The *S*s were male hooded Norway rats of the Lister strain, aged about 10 weeks. They were provided throughout with ample food and water in their home cages.

EXPERIMENT I

Part 1

Procedure. In this part of the experiment, the exploration box was empty. The aim was to study the exploration of one particular part of an empty box (the alcove) both in the course of one exploration period and on successive days. Each of 18 animals was therefore accustomed to handling during the two weeks prior to the experiment and then placed in the empty exploration box for 10 min. at a time on three successive days. In preparation for part 2, the animals were divided at random into three equal groups N, F, and O. The animals of group F were placed in the pre-exposure box with a 1-in. unpainted wooden cube for 10-min. after each of their three spells in the exploration box. For purposes of control, the *S*s of the other two groups were likewise placed in the pre-exposure box for 10 min. after each of their trials, but for them the cube was absent. Both boxes had interiors painted gray.

Results. The *time* per approach proved to be highly variable in a way that bore no clear relation to experimental conditions, and so it will not be mentioned hereafter. A split-plot analysis of variance for trend (1) was performed on the numbers of approaches, and its details are displayed in Table 1. The data were recorded for the first minute, the next 2 min., and the remaining 7 min. of each 10-min. trial. Consequently, the numbers of approaches for the second and third of these subperiods were divided by 2 and 7, respectively, for the within-trials analysis. Then, since this treatment could be expected to produce nonhomogenous variances, within-trials data underwent a transformation: $x \rightarrow 100 \log (1 + x)$ before being analyzed.

TABLE 1

Experiment I, Part 1

A. Whole-plot (between-trials) analysis of variance

Source	*df*	Mean square	*F*
Over-all slope	1	747.1	49.81***
Over-all deviations from linearity	1	343.0	22.87***
Individual means	17	40.0	2.67*
Individual slopes	17	79.6	5.31**
Individual deviations from linearity (error)	17	15.0	
Total	53		

B. Subplot (within-trials) analysis of variance (transformed data)

Source	*df*	Mean square	*F*
Subperiods	2	14261	57.04***
Subperiods × trials	4	690	2.76*
Subperiods × rats	34	343	
Residual (error)	68	250	
Total	108		

*** $p < .001$
** $p < .01$
* $p < .05$

C. Mean approaches per minute

	Trial 1	Trial 2	Trial 3	All trials
Subperiod 1 (1 min)	3.3	2.5	1.7	2.52
Subperiod 2 (2 min.)	2.0	0.5	0.3	0.95
Subperiod 3 (7 min.)	1.2	0.3	0.6	0.72
Whole trial (10 min.)	1.58	0.59	0.68	0.95

The following emerge clearly from the results:

1. There is a sharp drop in exploration from the first day to the second but not from the second to the third. This can hardly be explained by the presence of the screw after trial 1, as the screw was too small to affect *S* unless *S* attempted to sit, and discouraging sitting would increase rather than decrease the number of approaches.

2. Exploration declines steeply during each 10-min. trial with a concave-upward curve.

3. The proportion of the total exploration performed in the first minute increases on successive days.

Part 2

First Trial

Procedure. The second part of the experiment studied exploration of the 1-in. unpainted wooden cube in the alcove.

On the day after the third trial of part 1, each animal was placed in the pre-exposure box for 3 min. Group F were there exposed to the cube, while the box was empty for the other groups as before. Then, after an interval of 10 min., each *S* was placed in the exploration box for the first 3-min. trial of part 2. But the three groups were tested under different conditions, designed to provide information on the arousal of curiosity by novel objects.

For group N, the alcove contained the cube, and this was for them a completely novel object.

For group F, the alcove contained the cube, and this was a familiar object which they had met before during their four spells in the pre-exposure box, but it was also a relatively novel object inasmuch as they had never before seen it in its present setting.

For group O, the alcove was still empty, and so they constitute a control group.

Results. The number of approaches made by each *S* in the 3 min. of the first trial, part 2 was compared with the number made during the first 3 min. of the last trial of part 1. Only for group N was there a significant increase ($t = 3.55$, $p < .01$). Next, both the increases from the first 3 min. of the last trial, part 1, to the first trial, part 2, and the numbers of approaches in the first trial, part 2, were compared for the three groups. There are significant differences between group N and group O (mean increases = 5.5 [N], 2.2 [O]; $t = 2.41$; $df = 10$; $p < .05$; mean approaches = 7.2 [N], 4.0 [O]; $t = 2.17$; $df = 10$; $p < .05$ for one tail). The data for group F are midway between those for the other groups and not significantly different from either.

TABLE 2

Experiment I, Part 2

A. Analysis of variance (between trials)

Source		df	1 minute		3 minutes	
			Mean square	F	Mean square	F
Over-all slope		1	19.6	5.76*(c)	10.0	
Over-all deviations from linearity		2	4.6		19.2	2.02(c)
Group means	M/D	1	47.5	5.59*(a)	86.7	2.82(a)
	N/F/O	2	0.5		27.2	
	Interaction	2	12.3		16.4	
Group slopes	M/D	1	34.8	8.92*(b)	19.6	2.71(b)
	N/F/O	2	4.2		12.7	
	Interaction	2	12.3		1.9	
Group deviations	M/D	2	10.2	3.00(c)	17.1	
	N/F/O	4	5.7		30.8	3.24(c)
	Interaction	4	7.7		26.1	2.75(c)
Individual means (Error a)		12	8.5	2.50*(c)	30.7	3.23**(c)
Individual slopes (Error b)		12	3.9		7.2	
Individual deviations (Error c)		24	3.4		9.5	

** $p < .01$
* $p < .05$

B. Means

		Trial				All trials
		1	2	3	4	
1 min.	M	4.4	2.6	1.2	1.1	2.3
	D	3.6	4.8	3.7	4.0	4.1
3 min.	M	6.9	4.2	3.3	4.0	4.6
	D	6.2	8.0	5.3	7.6	6.8

We have therefore established that the group with a completely novel object explored more than the group with no object. But we have no answer to the question whether this difference is due to the fact that the object had never been met before, to the fact that it had never been met in that setting, or to the fact that it provided more stimulation—visual, kinesthetic, tactual, olfactory—than the empty alcove.

Four Trials

One implication of our Postulate (*b*), with the assumption that the satiation of curiosity is analogous to inhibition as described by Hull, is that massed trials will produce a more marked decline in exploration than distributed trials. The remainder of part 2 of Experiment I was intended to test this prediction. Three rats from each of the groups were allotted at random to condition D and three to condition M. This produced a 3 × 2 factorial design. The *S*s for condition D received four 3-min. trials with the cube in the exploration box at approximately 24-hr. intervals, while condition M meant four 3-min. trials at 10-min. intervals. For groups N and F, these four trials included the first trial for part 2, which has already been discussed. Since group O did not have the cube in the exploration box on this first trial, they were given four trials, massed or distributed, with the cube, beginning on the next day.

Results. An analysis of variance for trend was carried out on the numbers of approaches in whole 3-min. trials and also on the numbers of approaches in the first minute of each trial. The details appear in Table 2. A subplot analysis was also undertaken to compare the approaches made in successive minutes within trials, the means being 3.2 for the first minute, 2.0 for the second, and 0.9 for the third. The significant F's in the subplot analysis are for minutes ($F = 39.6$, $df = 2, 96$, $p < .001$) and for minutes × conditions M or D ($F = 5.81$, $df = 4, 96$, $p < .01$).

If the first-minute approaches for the 9 *S*s undergoing condition M are considered separately, the difference between trials is significant ($F = 5.56$, $df = 3, 24$, $p < .01$). But the corresponding F for those undergoing condition D is not significant, and so no decline with 24-hr. intervals is apparent.

The results therefore show once again a pronounced decrease in exploration in the course of trials. The prediction of a difference between massed and distributed trials is confirmed, but only with the data for the first minutes. It seems, therefore, especially in the light of what we found in part 1, that the satiation of curiosity is shown most sensitively by what happens in the first minute of exploration.

EXPERIMENT II

Part 1

Experiment 1 left some important questions unsettled, which suggest some further variables that may be worth investigating. First, there remains the question of absolute and relative novelty. We have still not established whether a rat's curiosity is diminished by its having met the object before in *any* setting or only by its having encountered it in its *present* setting. One function of part 1 of Experiment II was accordingly to study further the effect of pre-exposure to the test object in a different setting.

Secondly, we have the problem of whether satiation survives a 24-hr. rest. In part 1 of Experiment I (with the exploration box empty), we found clear evidence of a decline in exploration from one day to the next, but in part 2 (with the object) there was none. Various hypotheses to account for this discrepancy suggest themselves and indicate variables that call for investigation:

1. The fact that trials in part 1 lasted 10 min., while those of part 2 lasted 3 min., may have been responsible for the difference. A critical amount of curiosity reduction necessary for a permanent decrement may require more than 3 min. to be reached.

2. Since the empty alcove resembled the rest of the exploration box more than the unpainted cube did, satiation generalizing from exploration of the rest of the box might have enabled a critical amount of curiosity reduction to be reached more easily in part 1.

3. The curiosity aroused by an object, with its multiplicity of stimuli, might take longer to satiate than that aroused by an empty alcove. If so, a critical amount of curiosity reduction may not be reached by the end of a trial. Welker (23) found that objects presenting more complex and more heterogeneous stimuli are explored more readily by chimpanzees.

4. A permanent decline in exploration may follow only a rat's first experience of a particular situation. Only the first experience may occasion a critical amount of curiosity reduction.

Part 1 of Experiment II tested the first and second of these hypotheses by using a 10-min. test period with an object, and by comparing exploration of an object painted the same color as the interior of the box with that of an unpainted object.

Procedure. Twenty *S*s were pretested by being placed in the empty exploration box for 3 min. and having their approaches to the alcove recorded. They were then divided into five levels of four rats according to the number of approaches made, and one rat from each level was allotted randomly to each of the four experimental groups—NG, PG, NU, PU. On each of the following five days, every *S* was given a 10-min. spell in the pre-exposure box and, immediately afterward, a 10-min. test-trial in the exploration box with an object. The interior of the pre-exposure box was painted black.

Two objects were used, namely, an unpainted wooden 1½-inch cube and a similar cube painted the same shade of gray as the interior of the exploration box. Groups NU and PU were tested with the unpainted cube, and groups NG and PG with the gray one. Groups PU and PG had in the pre-exposure box a cube of the same color as the one with which they were to be tested, while groups NU and NG had the cube with which they were not to be tested.

Results. Analyses of variance for trend, similar to those shown in Table 2, were performed on the numbers of approaches in 10-min. trials and in the first minutes. Of the comparisons in which we are interested, the only one to show a significant F was that for 10-min. data between group means of rats tested with the unpainted cube and rats tested with the gray cube. The mean approaches per trial were 19.9 to the unpainted and 12.8 to the gray cube ($F = 5.40$, $df = 1, 16$, $p < .05$). The corresponding data for the first minute yielded no significant difference. None resulted from pre-exposing *S*s to the test cube in the pre-exposure box as distinct from pre-exposing them to a different cube, and none emerged between successive trials on different days. We are still left, therefore, with two problems requiring further study.

Part 2

The second part was concerned with the effect of confronting a rat in the exploration box with a different object from the one *S* had explored there on at least five previous days. Would the change produce an increment in curiosity?

Procedure. On each of the two days following part 1, every *S* was given a 3-min. trial in the exploration box. One trial was with the object that had been used in part 1, and the other was with a different object. For groups NU and PU, the new object was a black cube (which they had never met before), and for groups NG and PG it was an unpainted cube (which they had never met before in the exploration box but had met in the pre-exposure box). Groups PG and NU had the new object on the first day and the familiar object on the second, and the order was the reverse for groups NG and PU.

Results. No significant differences appeared in the course of a split-plot analysis of variance either between new-object and familiar-object conditions or in connection with any other variables. The change did not therefore produce an increment in curiosity; there were actually slightly more approaches to the familiar than to the new object (means = 7.2 and 5.4, respectively). It may be worth noting that approaches decreased, but not significantly, from the first to the second day (means = 7.6 and 5.0, respectively).

Part 3

Part 1 failed to support the first and second of the hypotheses that were cited with reference to the persistence of satiation after a 24-hr. interval. Part 3 was therefore carried out with a view to testing the third hypothesis, namely, that an object presenting a variety of stimuli may arouse more curiosity than an empty alcove. At the same time, it was deemed worth while to investigate whether holding an animal in the narrow confines of the pre-exposure box immediately before testing has any effect on subsequent exploratory activity. This question is of interest in the light of Montgomery's failure to find a relation between exploration and a general activity drive (17).

Procedure. All *S*s were given a 10-min. trial in the exploration box on each of the two days following part 2. Groups NU and PU were tested with a gray cube which they had never seen before, and groups NG and PG were tested with the alcove empty (which it had not been during the past seven days). Groups PU and NG were confined in the empty pre-exposure box for 10 min. before each trial, but groups NU and PG were taken to the exploration box from a large and roomy cage.

Results. Analyses of variance were carried out on 10-min. and first minute data. The *S*s that were tested with a cube in the alcove explored significantly more than those tested with the alcove empty, according to first-minute data (means = 3.4, 2.8, respectively; $F = 5.10$; $df = 1, 19$; $p < .05$). The corresponding difference between 10-min. data just misses the .05 level of significance (means = 18.4, 11.2; $F = 4.24$). There was no appreciable difference between *S*s confined in the pre-exposure box before testing and the others, a finding consonant with Montgomery's. However, a split-plot analysis of the first-minute data revealed a significant decrement from the first day to the second (means 3.9, 2.3; $F = 13.7$; $df = 1, 16$; $p < .01$).

EXPERIMENT III

Part 1 of Experiment II showed that more approaches were directed to an unpainted than to a gray cube. This may have been due to differences in odor or to the fact that the unpainted wood resembled the animals' food. If so, no issue of great theoretical interest arises. But it is also possible that differences in brightness are involved, and this was deemed a variable worth investigating. Since the unpainted cube was lighter than the gray one and also contrasted more with the rest of the interior of the exploration-box, we have two distinct variables to manipulate separately.

Secondly, part 1 of Experiment II failed to show that *S*s that have been pre-exposed to the test object immediately before each trial explore it less than *S*s that have been pre-exposed to a different object. But our theory requires that pre-exposure should have some effect. There might well have been too much stimulus generalization between a gray and an unpainted cube for the difference to appear. It was therefore held worth while to give the prediction a more thorough investigation by comparing the effect of pre-exposure to the test-object with that of pre-exposure to an empty pre-exposure box.

TABLE 3

Experiment III

A. Analysis of variance

Source	*df*	5-min. data		First-minute data	
		Mean square	*F*	Mean square	*F*
Group (W′ or G′)	1	160.2	2.84(a)	51.0	6.30*(a)
Subjects (Error a)	22	56.4	3.85**(b)	8.1	2.87**(b)
Color of object	1	4.2		0.4	
Pre-exposure	1	13.5		9.4	3.33†(b)
Color × pre-exposure	1	15.1		1.5	
Days	3	14.6		6.9	2.44(b)
Color × group (Contrast)	1	1.1		0.0	
Pre-exposure × group	1	0.4		0.7	
Days × group	3	16.2		1.0	
Color × pre-exposure × group	1	24.0		0.0	
Residual within subjects (Error b)	60	14.7		2.8	
Total	95				

** Significant at .01 level.
* Significant at .05 level.
† Significant at .05 level by one-tailed test.

B. Means

	Day				All days
	1	2	3	4	
First minute	3.8	2.8	2.6	2.7	2.96
5 minutes	7.0	6.0	5.3	5.3	5.90

Procedure. Twelve rats (group G′) were tested with the exploration box painted gray inside, as in the other experiments. But the color of the interior was changed to white for group W′ (12 rats). Each *S* underwent a different one of four treatments on each of four successive days. The treatments were: (*a*) 5 min. in the *empty* pre-exposure box followed by 5 min. in the exploration box with a *gray* 1½-in. cube; (*b*) 5 min. in the pre-exposure box with a *gray* cube followed by 5 min. in the exploration box with a *gray* cube; (*c*) 5 min. in the *empty* pre-exposure box followed by 5 min. in the exploration box with a *white* 1½-in. cube; (*d*) 5 min. in the pre-exposure box with a *white* cube, followed by 5 min. in the exploration box with a *white* cube. Different rats received the treatments in different orders, so that the design for each group took the form of three 4 × 4 latin squares whose columns represented individual *S*s and whose rows represented different days. The latin squares were planned in such a way that every treatment immediately preceded and succeeded every other treatment an equal number of times. *S*s of group W′ were 8–13 days older than those of group G′.

Results. Both the data for whole 5-min. trials and data for first minutes were submitted to a split-plot analysis of variance (Table 3). It will be seen that neither the albedo of the test-object nor the contrast between its albedo and that of its setting produced an appreciable effect. Pre-exposure to the test object, if we halve the probability given in the usual *F* table on the grounds that a prediction in a definite direction was made, produced the expected effect according to the first-minute data at the .05 level of significance. The first-minute means were 2.6 approaches with pre-exposure to the test object and 3.3 without.

The first-minute data also show that group W′ explored the objects more than group G′ (means = 3.7, 2.2, respectively). Our experimental design, which confounded age of *S*s with color of the exploration box, does not allow us to decide from our results which of these two variables is responsible for this difference. But the findings of other experimenters supply a probable answer to this question. Montgomery (17) reports that his rats engaged in about equal amounts of exploratory behavior whether they were in a white maze or a black maze. On the other hand, it is known that the general activity of the rat increases steeply with age up to at least the beginning of the fourth month (20).

Although the analysis of variance does not exhibit a significant difference between approaches on different days, an inspection of the means reveals a tendency for exploration to decrease, especially after the first day. Actually, 16 *S*s showed a decrease from the first minute of the first day's trial to the first minute of the second day's trial, and four showed an increase. This trend is significant at the .01 level by the sign test. But no such trend is visible after the second day. It looks, therefore, as if a permanent decrease in curiosity is mainly in evidence after the rat's first exposure to a situation. This agrees with the findings of Watson (22), whose rats were strikingly less emotional and less generally active after their first experience of an experimental situation even when several weeks elapsed before their second experience. Experiment III thus confirms the existence of a lasting decline in exploratory activity after the first trial, which we also found in part 1 of Experiment I. The failure of this decline to manifest itself in Experiment II may be attributed to the fact that the *S*s were placed in the exploration box for 3 min. to determine initial exploration levels before participating in that experiment. They therefore had their first experience of the situation before the test trials began, and the fourth of our hypotheses to account for the nonappearance in Experiment II of a permanent decrement in exploration seems to have been supported.

SUMMARY AND DISCUSSION

Our three experiments have sampled the effects of several of the variables that might be thought to influence the number of approaches made by a well-fed and well-watered rat to a particular item in its environment. The positive and negative results obtained may be summarized as follows, the relevant experiments and parts of experiments being indicated in parentheses.

A finding concerning the *arousal* of curiosity was:

1. A part of the environment presenting numerous and complex stimuli is explored more than one presenting few and simple stimuli (II, 3; and possibly I, 2 and II, 1).

Findings concerning the *satiation* of curiosity were:

1. A permanent decrement in exploration occurs after an animal's first experience in a situation (I, 1; III).
2. An object evokes less exploration if an animal has been exposed to it for 5 min. before testing (III).
3. There is a decline in exploration when the animal is given four massed trials at 10-min. intervals (II, 2).
4. The amount of exploration per minute decreases steeply according to a concave-upward curve in the course of a single trial (I, 1; I, 2; and confirmed by other experiments).
5. The proportion of exploration occurring in the first minute of a trial increases after an animal's first experience of a situation (I, 1).
6. The decline in amount of exploration in successive minutes of a trial is more pronounced with distributed trials separated by 24-hr. intervals than with massed trials separated by 10-min. intervals (I, 2).
7. There may be a further permanent decline in exploration after daily trials for a week (II, 3).

Variables which were not found to influence the amount of exploration were:

1. A change in one feature of an environment that the animal has explored several times previously, the last time being 24 hr. ago (II, 2).
2. The albedo of an object (III).
3. The difference in albedo between an object and its setting (III).
4. Whether or not the animal is confined in a small box for 10 min. before being tested (II, 3).
5. Whether the animal is exposed, just before testing, to an object identical with the test object or to one differing from it only in albedo and possibly odor (II, 1).

Some tentative conclusions suggest themselves:

1. In view of the apparently permanent decline in curiosity after a first trial, the application of a two-factor theory of inhibition to the satiation of the curiosity drive is not ruled out. It would seem, however, that some such modification as that introduced by Kimble (13) to cover the facts of motor learning is required, i.e., the permanent component of satiation will only be manifest in certain circumstances. One possibility is that the amount of curiosity reduction must exceed a threshold value.

Welker's chimpanzees (23) showed a decrease in responsiveness to particular objects over periods of several days up to a month. It is noteworthy that Welker's experiments, like our own, tested exploration of individual objects, whereas Montgomery (17), who failed to find a day-to-day decline, observed exploration of parts of a maze. We can only hazard the suggestion that maze runways present a large assortment of stimuli, so that a 10-min. exploration period may not allow enough time to satiate the curiosity aroused by most of them to the point at which a permanent decrement appears.

2. Apart from the decline after the animal's first experience of a situation, curiosity seems to be aroused mainly by *short-term novelty*, i.e., by something different from what it has been perceiving during the past few minutes. We found no evidence that exploration is affected when there is change in one feature of an environment that *S* has encountered several times before but not within the last 24 hr. On the other hand, as our previous experiments showed (2), an object that was not in the situation 10 min. ago provokes more exploration than one that was. The perceptual curiosity drive may thus be more closely related than we thought (2, p. 71) to the "investigatory reflex" mentioned by Pavlov (19, p. 12).

3. Since we so often found significant results with the data for the first minute spent in the exploration box and not for the data for whole trials, and since a disproportionate amount of exploration always occurred in the first minute, it looks as if an animal's earliest moments in a new situation have a particular importance. The principal variables that we have found to influence the degree of curiosity aroused seem largely to concern the first minute, and thereafter exploration seems to depend much more on chance factors.

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DAILY PATTERNS OF VISUAL EXPLORATORY BEHAVIOR IN THE MONKEY[1]

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Rhesus monkeys learn color-discrimination problems when correct responses are rewarded by the opportunity to engage in visual exploratory behavior (1). Moreover, on discrimination learning problems, Butler and Harlow (3) have demonstrated that monkeys respond persistently to visual incentives throughout many continuous hours of testing. In these studies, *E* controlled the times at which the stimuli were presented, and latency of the *S*'s responses to the stimuli was taken as the measure of motivational strength. The *E* also imposed a 30-sec. limit on the duration of visual exploratory behavior following correct responses.

Although these testing techniques have provided valuable data on the visual exploratory behavior of monkeys, they are not designed or precisely adapted for investigating motivational strength. Some brain-damaged animals, for example, responded consistently and rapidly but spent only a small fraction of each allotted 30-sec. period visually exploring the surrounding environment (3). There was no apparent effect on response latencies of the *S*'s success or failure on problem solution; nevertheless, it is desirable to eliminate discrimination problems from the testing situation when the emphasis is to be placed on the persistence of visual exploratory responses.

The present experiment was designed to provide more direct measures on the motivational strength of visual exploration by use of an apparatus in which the *S*s were permitted to control both frequency and duration of responses throughout prolonged and repetitive test sessions.

METHOD

Subjects

Six immature rhesus monkeys (no. 301, 302, 303, 304, 305, and 306), whose weights ranged from 5 to 7 lb., served as *S*s. None of the animals had had previous laboratory testing experience.

Apparatus

The monkeys were tested in an enclosed aluminum cage measuring 26 by 16 by 30 in. An aluminum door, 3¼ in. sq., was centered on the front of the cage with its base 11 in. above the floor of the cage. A vertical metal arm was attached to the door and extended 3 in. above the cage. A spring was connected to the extended arm of the door and to the top of the cage in order to hold the door in the closed position. With the door closed, the extended arm contacted and depressed a normally closed microswitch situated on the top of the cage. When the monkey pushed open the door, the microswitch reverted to its normal position, which in turn activated a counter and a running time meter. As soon as the monkey stopped holding the door open, the action of the spring closed it immediately, thereby depressing the microswitch and stopping the running time meter. With this arrangement, the frequency and duration of responses were recorded automatically. A 25-w. lamp attached to the roof of the cage provided illumination within. The inside of the cage was painted black and the door white. The monkeys were introduced into the test apparatus through a sliding door located at the rear. Testing was conducted in a room housing a colony of approximately 30 rhesus monkeys, including those that participated in the experiment.

Procedure

Preliminary training served to adapt the monkeys to the test apparatus. For the first several preliminary training sessions the animals were housed in the cage with the door fixed in the open position. As soon as the monkeys appeared to be adapted to the cage and remained in front of the open door rather than staying in the rear of the cage, they were trained to open the door when it was completely closed. Three of the animals learned this without special training. For the other monkeys, it was necessary first to unhook the spring from the door, then close the door part way. When the monkey responded by pushing the door open, *E* closed the door further. Within a few trials, monkeys were pushing open the door when it was completely closed, and continued to do so after the spring had been attached, thereby completing preliminary testing.

Formal testing consisted of testing each monkey 10 hr. a day continuously on six consecutive days. Frequency and duration of responses were recorded. The test sessions always began at approximately 8:00 A.M. The animals were fed a standard laboratory meal 30 min. before being tested. Water was always available inside the cage.

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[1] The authors wish to express their appreciation to Capt. Joseph V. Brady, U.S.A., and Dr. Murray Sidman, Army Medical Service Graduate School, for their cooperation in this experiment.

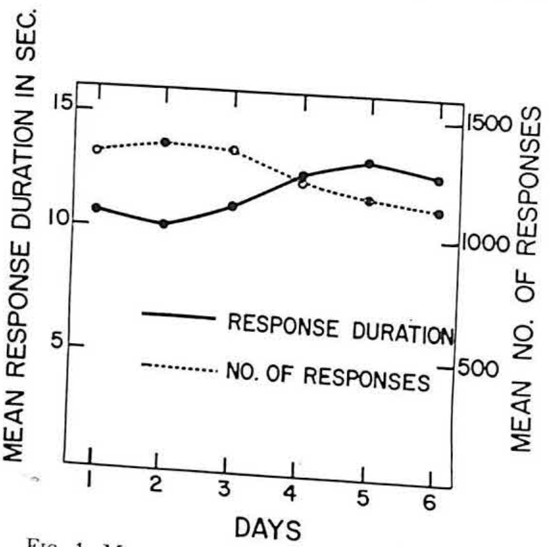

FIG. 1. Mean response duration and mean number of responses as a function of days.

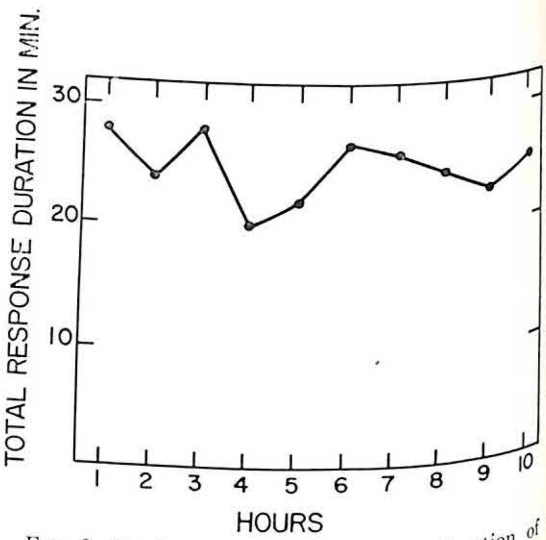

FIG. 3. Total response duration as a function of hours within days.

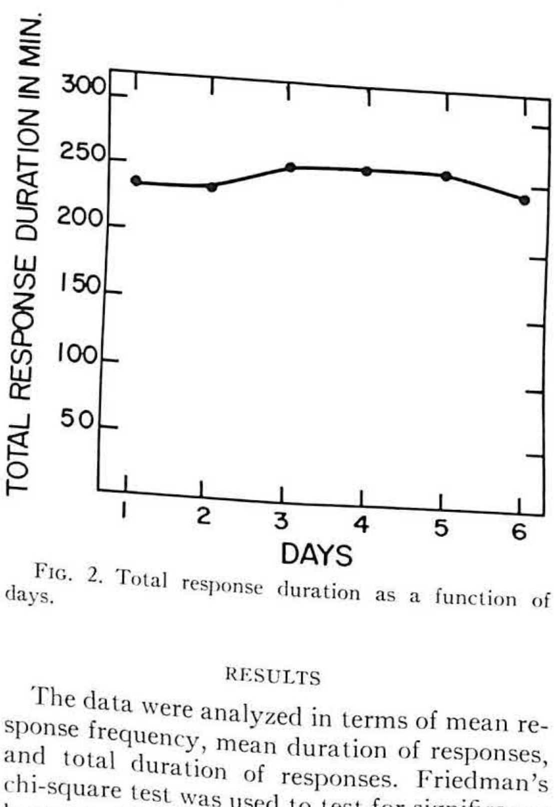

FIG. 2. Total response duration as a function of days.

RESULTS

The data were analyzed in terms of mean response frequency, mean duration of responses, and total duration of responses. Friedman's chi-square test was used to test for significance between days and between hours within days.

Figure 1 shows mean number of responses and mean duration of responses as a function of days. Response frequency tended to decrease as the experiment progressed, but the duration of responses appeared to increase. No significant differences in mean response frequency were found between days, but differences in mean duration of responses were significant beyond the .05 confidence level. Figure 2 shows the total duration of responses averaged for the six *S*s, and these data suggest that monkeys worked to attain a relatively fixed amount of daily visual exploratory experience by manipulating the two variables under their control, viz., response frequency and the duration of each response. The mean of the daily total response durations was 246.7 min., with a standard deviation of 47.3 min. Total response durations ranged from 181 to 331 min. That the total daily response duration recorded for the *S*s averaged more than 4 hr., is indeed a striking demonstration of the motivational strength of visual exploration.

Figure 3, in which total duration of responses is plotted as a function of hours within days, illustrates the marked fluctuations in the amount of visual exploratory behavior recorded for the various hours, and these differences were significant at the .05 level. There was, however, no consistent increase or decrease in any of the measures of responsiveness from hours 1 through 10.

The marked variations in the amount of visual exploratory behavior recorded for hours within days appeared to be related to the activity occurring in the colony. For example during the first test hour of each day several people usually entered the testing room to conduct routine tasks. During the third test hour, the colony was fed. Feeding continued for about 40 min. and was always accompanied by vigorous vocalizations by the monkeys of the colony. During hours 4 and 5, the colony was quiet, but it usually became more active during the latter part of the day.

DISCUSSION

The results of this experiment testify to the strength of visual exploratory behavior in the rhesus monkey. During prolonged and repetitive test sessions, the animals performed persistently, showing no evidence of satiation. Total duration of responses appeared to be the most stable measure of responsiveness, remaining remarkably constant for each of the six days, while response frequency and duration of individual responses varied considerably.

Observational data suggest that auditory stimuli are important in eliciting visual exploratory responses. In many instances the animal pushed open the door immediately following fight sounds within the colony, the noise produced by a monkey shaking its cage, or the sound of the test-room door opening and closing. The role of auditory stimulation in evoking visual exploratory behavior, however, cannot be determined from this experiment.

The significant intraday variation of visual exploratory behavior is attributed to changes in the incentive conditions. This appears to be a reasonable interpretation of these data since different visual incentive conditions can significantly influence the frequency of visual exploratory responses (2).

CONCLUSIONS

Six experimentally naive rhesus monkeys were tested 10 continuous hours a day for six consecutive days on a simple task to visual incentives. The frequency and duration of responses were controlled by the *S*s and were recorded automatically.

The results clearly demonstrated the effectiveness of visual and auditory incentives in eliciting and maintaining visual exploratory behavior. An average of 40 per cent of the total testing time was spent in visual exploratory behavior. The data suggested that the animals worked to attain a relatively fixed amount of daily visual exploratory experience.

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THE EFFECT OF FOOD DEPRIVATION ON EXPLORATORY BEHAVIOR IN A COMPLEX MAZE

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The results of two recently published experiments have questioned the long-held assumption, indirectly supported by many activity-wheel and activity-cage studies, that such primary drives as hunger and thirst increase exploratory behavior in the white rat. Montgomery (7), using a single-unit Y maze placed in a small, curtained enclosure found that deprived female rats actually explore less than sated rats. Thompson (9), using a rectangular maze with a path across the center and also placed in a uniformly curtained enclosure, found few significant differences between hungry and sated groups although some sex differences were apparent.

These results are at variance with the only other published paper dealing with the relation between food deprivation and maze exploration. In 1925, Dashiell (2) reported the results of a class demonstration in which hungry and sated rats were placed in a Dashiell open-alley maze located in a laboratory room with students standing around tracing the rats' movements on mimeographed copies of the maze. In the 60-sec. exploration period, 17 hungry rats traversed, on the average, 42.9 units 10 cm. long whereas the 17 controls traversed only 26.7 units.

The chief difference between the Montgomery and Thompson and the Dashiell experiments lies in the far greater variety and complexity of environmental cues, both within- and extra-maze, provided in the latter study. The difference in findings suggests that hunger lowers the reaction level to extensive and varied novel external stimuli but has little effect when the novel cues are few.

The thesis that hunger lowers the reaction threshold to novel stimuli is supported in a recent study by Campbell and Sheffield (1), who have shown that the increased activity of hungry rats in activity-cage studies is probably a function of the presence of external stimulation and not exclusively of internal states. When placed in a highly restricted environment, their hungry and sated rats differed little in activity, whereas when new stimuli were introduced, they were far more active when hungry. The data clearly support their conclusion that "hunger drive seems to involve lowered thresholds of response rather than internal stimulation to activity" (1, p. 321).

Indirect additional support for this thesis may be found in a recent study by Murray (8). He measured the effect of hunger on rate of unrewarded responding in Skinner boxes equipped with three different types of manipulandum: a short bar, a long bar, and a chain. The finding that hunger increased response rate to the two latter types but not to the former type suggests that highly discriminable (novel?) external cues have a more stimulating effect on hungry rats whereas less discriminable cues do not affect hungry and sated rats differently.

On the basis of this hypothesis it would follow that in a maze offering a profusion of spatially separated new stimuli the hungry and therefore more sensitive animal should be more readily diverted from the stimulus it is now exploring to a new one. It should therefore traverse more maze units in a given period of time than the sated rat. On the other hand, in a very simple homogeneous maze allowing for much stimulus generalization and therefore little novelty after the first minute or so, the hungry rat might not be more easily diverted.

The present experiment was designed to test the effect of hunger on exploratory activity in a complex maze located in a room providing varied extra-maze cues. For the reasons cited above it was assumed that, as in the Dashiell demonstration, hungry rats would explore more than sated rats.

METHOD

Subjects

The *Ss* were 23 naive male albino rats of Wistar strain. They were approximately 90 days old at the beginning of the experiment.

Apparatus

The appratus consisted of a multiple-alley maze (Fig. 1) having an irregular pattern. The maze was placed on a table in the center of the room containing the *Ss'* living cages. Extra-maze cues included a light fixture located 4 ft. above the maze center, a window, door, cabinets along one wall, and the top tier of cages. The *E* sat in one corner of the room from which he could see the rats in all parts of the maze.

The maze was constructed of small units each 4.5 in. long. The unit of measurement for exploratory activity was the 4.5- by 4.5-in. square bounded by a pair of these units. Timing was by means of a Kodak timer, and the performance of the *Ss* was recorded by tracing the path taken on mimeographed copies of the maze.

The *Ss* were housed throughout the experiment in individual cages each having 160 sq. in. of floor space.

Procedure

The *Ss* were divided at random into two groups each of which was given three 10-min. tests of exploration in each of the three parts of the experiment. Group HSS ($N = 12$) was tested successively under the motivating conditions of hunger, satiation, and satiation. The comparable motivating states for Group SSH ($N = 11$) were satiation, satiation, and hunger. The detailed outline of the procedure follows. All rats had free access to water throughout the experiment. No food or water was ever placed in the maze.

Days	
1-2	Handling and taming. Free access to food.
3-6	Adaptation of Group HSS to maintenance schedule. Group HSS on daily ration of 7 gm. of Rockland rat diet. Group SSH free access to food.
7-9	*Part A.* Daily 10-min. test of exploratory activity. This was divided into five consecutive 2-min. periods. Group HSS on 7-gm. daily ration. Group SSH free access to food.
10-14	Rest. Free access to food for all *Ss* to enable Group HSS to restore weight lost on days 3 to 9.
15-17	*Part B.* Daily 10-min. test of exploratory activity. Both groups free access to food.
18-21	Adaptation of Group SSH to maintenance schedule. Group SSH on daily 7-gm. food ration. Group HSS free access to food.
22-24	*Part C.* Daily 10-min. test of exploratory activity. Group SSH on 7-gm. daily ration. Group HSS free access to food.

The *Ss* were always placed at point *X* in the maze. Timing and exploratory behavior were recorded from the moment *S* passed point *Y*. The criterion for exploration of a unit was a head-and-shoulder entry. At the end of the 10-min. period *S* was returned to its home cage from wherever it happened to be in the maze. *Ss* run hungry were fed their daily ration at least ½ hr. after removal from the maze.

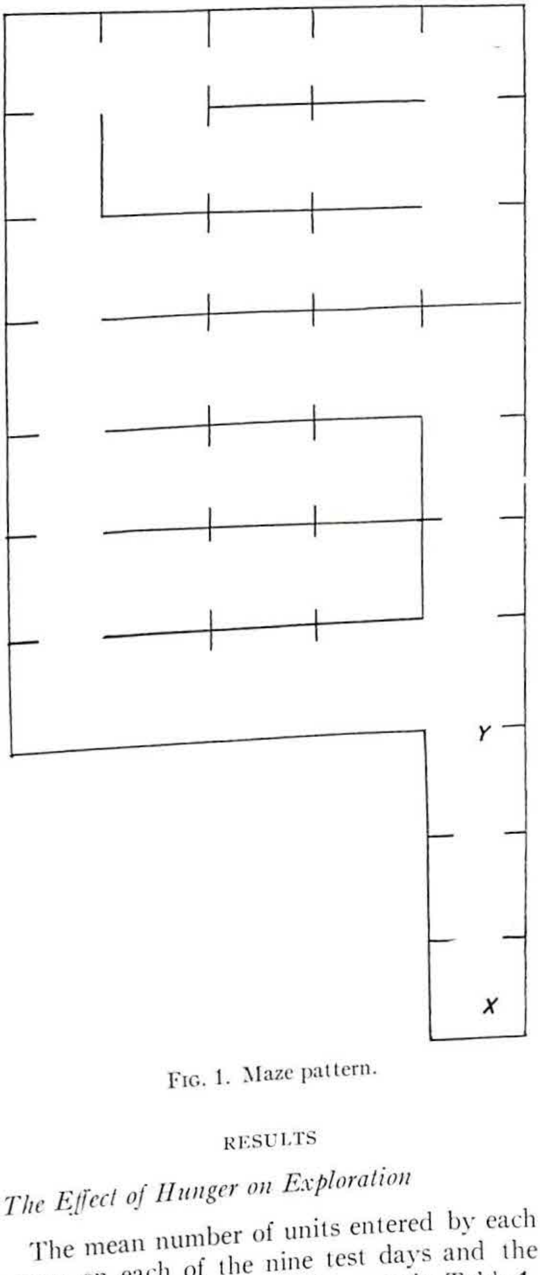

FIG. 1. Maze pattern.

RESULTS

The Effect of Hunger on Exploration

The mean number of units entered by each group on each of the nine test days and the means for Parts A, B, and C appear in Table 1. The data show clearly that hunger increases the amount of exploration. In Part A Group HSS explored 77 per cent more units than Group SSH; in Part C Group SSH explored 53 per cent more than Group HSS. These differences are significant well beyond the .01 confidence level.

Differences in favor of the hungry group which are significant at the .05 level or beyond were found on each of the individual test days

TABLE 1

Mean Number of Maze Units Explored on Each Test Day

	Group HSS	Group SSH	t	p
Part A				
Day 1	238	189	1.57	
Day 2	234	111	3.80	.001
Day 3	279	134	3.82	.001
Mean	250	144	3.78	.01
Part B				
Day 1	187	130	1.89	
Day 2	185	158	0.89	
Day 3	162	120	1.17	
Mean	178	136	1.52	
Part C				
Day 1	179	241	2.19	.05
Day 2	158	229	2.14	.05
Day 3	136	252	3.68	.01
Mean	157	240	2.96	.01

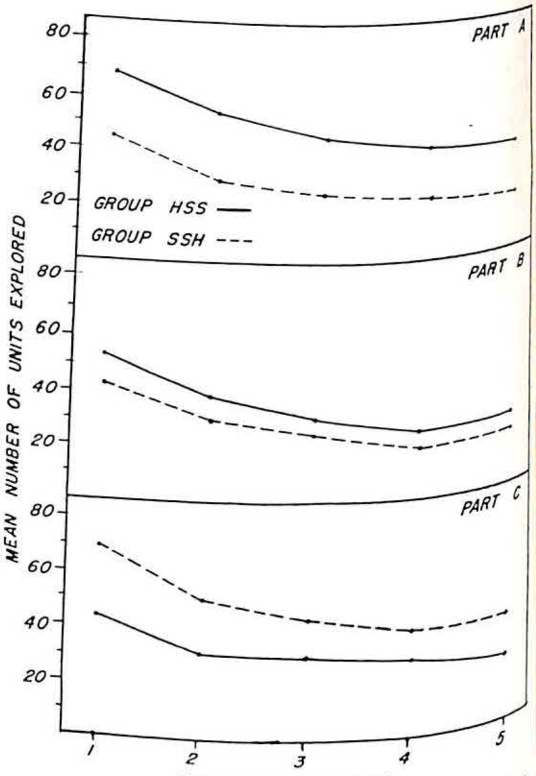

FIG. 2. Mean number of units explored in successive 2-min. intervals.

of Parts A and C with the exception of the first day. On this day the sated group, SSH, explored far more than it did on any other of the six days when run sated. The number of units entered by this group on the succeeding five test days did not differ significantly from each other. The fact that the maze was necessarily more novel on the first day may account for this difference in rate of exploration. Group HSS, however, did not show a comparable decline in activity during the three days of Part A. For this group decrease in novelty may have been counterbalanced by increased hunger drive as these rats lost approximately one-seventh of their original body weight during the seven days on which they were on reduced rations. They may therefore have become, as Campbell and Sheffield have shown, more reactive to the stimulation provided by this maze

Reading down the second and third columns of Table 1 shows that each group of *S*s was more active when hungry than when sated. For Group HSS the differences between Parts A and B and between Parts A and C are significant at the .01 level. For Group SSH the differences between Parts A and C and between Parts B and C exceed the .01 confidence level. On the other hand exploratory activity did not differ significantly in the two parts in which the motivating state was the same, i.e., Parts B and C for Group HSS and Parts A and C for Group SSH.

Satiation Syndrome

As the *S*s of Group HSS had explored so much more than those of Group SSH in Part A, it was believed that they might show evidence of Finger's satiation syndrome (4) in Part B and therefore explore less than Group SSH. The data show no such evidence of satiation. Although the differences between the groups on each of the three days of Part B show somewhat more activity for Group HSS, no difference approaches even the .10 confidence level. These data are in agreement with findings by Montgomery (6, 7) that there are no day-to-day changes in exploration when the internal motivating conditions of the *S*s are not varied.

Relation Between Amount of Exploration and Time in the Maze

On each test day there was a marked decline in activity with time spent in the maze. The mean number of units explored during each succeeding 2-min. period on the three days of each part are shown in Figure 2. Activity was at a peak during the first 2-min. period and dropped off at a declining rate in succeeding periods. The curves for hungry and sated *Ss* are comparable, indicating that internal motivating state does not affect the shape of the curve. This finding is quite in accord with the results of previously published studies on maze exploration (3, 5, 7, 9).

Consistency of Exploratory Behavior Within Days

Casual observation indicated that hungry *Ss* explored at a fairly consistent pace whereas the behavior of sated *Ss* showed spurts of activity separated by rather long pauses during which washing and napping frequently occurred. This observation was supported by two analyses of the data. First, a count of the number of 2-min. periods during which a rat failed to explore showed that such periods were far more frequent among sated *Ss*. For all the *Ss* of Group HSS there was 1 such period in Part A, 26 in Part B, and 30 in Part C. The comparable values for Group SSH were 38, 36, and 4. Second, the coefficient of variation, *V*, (100 *SD*/Mean) was computed for each rat for each day from the five daily 2-min. records. The mean *V*'s for Group HSS in Parts A, B, and C were, respectively, 31, 60, and 64; for Group SSH, 83, 81, and 34. During Part A, *V* was significantly larger for Group SSH ($p = .01$) while during Part C Group HSS was significantly more variable ($p = .05$). Both analyses support the observation that hunger is associated with a more consistent rate of exploration. This finding seems consistent with our initial assumption that hunger lowers the reaction threshold to novel stimuli. If, compared with sated *Ss*, the behavior of deprived animals is more under the control of external stimuli and if these are widely separated spatially, hungry rats should keep moving at a fairly steady rate. The actions of sated rats on the other hand may be relatively more influenced by varying and temporary internal conditions, and this could account for their greater frequency of washing, napping, and spurts of exploratory activity.

SUMMARY

A comparison was made of the exploratory behavior of hungry and sated rats in a complex, asymmetrical maze situated in a room providing highly differentiated extra-maze cues. Twenty-three rats were run under alternating conditions of zero- and 23-hr food deprivation. The major findings were:

1. Rats, when deprived, explore from 50 per cent to 75 per cent more units than when sated.
2. Previous motivating conditions and exploratory rates have little if any effect on current daily exploratory behavior.
3. There is a decrement in exploratory rate with time of exposure to a maze during each daily test. This decrement is similar in hungry and sated groups.
4. Deprived rats explore at a more consistent rate than sated rats.

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THE RELATION BETWEEN FEAR INDUCED BY NOVEL STIMULATION AND EXPLORATORY BEHAVIOR

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The purpose of the present investigation is to determine whether novel stimulation evokes the fear drive as well as the exploratory drive. A growing body of evidence indicates that novel stimuli evoke the exploratory drive (e.g., 2, 3, 8, 10, 13). Qualitative observation has repeatedly suggested to the author that such stimuli may also evoke the fear drive. In the psychological and zoological literature the same suggestion has been made a number of times, and scattered and unsystematic evidence supporting it can be found (e.g., 4, 5, 6, 12).

Available evidence indicates that the exploratory drive leads to approach behavior (1, 11) and that the fear drive leads to avoidance behavior (7, 11). If novel stimulation evokes both drives, it should generate an approach-avoidance conflict. One way of investigating this problem, then, is to devise a situation in which approach-avoidance behavior generated by novel stimulation can be measured. This is done in the first experiment reported below. A second way is to vary the strength of one drive while holding the strength of the other relatively constant in a situation where either approach or avoidance behavior, or both, can be measured. This is done in both experiments reported below.[1]

EXPERIMENT I

This experiment is designed: (*a*) to test, in a simple, single-choice situation, the hypothesis that novel stimulation evokes both the fear drive and the exploratory drive, thus generating an approach-avoidance conflict; and (*b*) to determine the effects on approach-avoidance behavior of varying the strength of the fear drive evoked by novel stimulation.

Method

Subjects. The *Ss* were 30 female albino rats of the Wistar strain. Ten animals were about 150 days old; five were assigned at random to Group I and five to Group II. Twenty rats were 80 to 90 days of age; five were assigned at random to Group III, Group IV, Group V, and Group VI. The animals in Groups I to IV were tamed prior to the experiment; those in Groups V and VI were not. All rats had free access to food and water at all times including the experimental sessions.

Apparatus. This consisted of (*a*) five living cages each 16 in. long, 12 in. wide, and 10 in. high, constructed from hardware cloth and a sheet-metal front wall containing in its center a sheet-metal, guillotine-type door 4 in. wide and 4 in. high, (*b*) an enclosed straight alley 6 ft. long and 4 in. wide, and (*c*) an elevated straight alley 6 ft. long and 4 in. wide. The mazes were constructed from unpainted white pine; the floor of each was covered with hardware cloth. The enclosed maze had a hinged hardware-cloth top. All pieces of apparatus were elevated 30 in. from the floor. One end of each maze could be placed immediately adjacent to the door of each living cage. For purposes of recording, the floor of each maze and living cage was marked off in 8-in. sections.

Procedure. Over the four days of the experiment the procedure was the same for all groups. On day 1 each rat was placed in one of the living cages and given a 24-hr. period of adaptation to the cage to extinguish its fear and exploratory-drive evoking properties. Preliminary research indicated that longer periods of adaptation were not necessary. Each cage contained food and water at all times. On days 2, 3, and 4 each animal was given one trial which consisted of opening the home-cage door and allowing it free access to either the enclosed or the elevated maze for 10 min. The rats in Groups I, III, and V were exposed to the enclosed maze; those in Groups II, IV, and VI, to the elevated maze. One group was run at a time, in the order indicated by the group numbers. No animal was handled after being placed in its living cage on day 1 until its three trials were completed. During the trials, *E* manipulated the living-cage doors and observed the animals from an elevated position about 6 ft. behind the living cages.

For each animal the total number of 8-in. maze sections traversed during each 2-min. period of exposure to a maze was recorded. Qualitative observation of the behavior of the rats in Groups I and II suggested two additional measures which were recorded for Groups III to VI: (*a*) the number of retreats from the front to the rear half of the living cage, and (*b*) the number of times each animal "looked away" from the open cage door after "looking into" the maze alley. A maze-section traversal was recorded when a rat made a full body-length entry, excluding its tail, into an 8-in. section. The same body-length criterion was used in recording entries into the front and rear halves of the living cage. A "look away" from the cage door was

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[1] Data on two of the ten experimental groups used in the present experiments were collected by Marshall Segall.

TABLE 1

Summary of the Results of Experiment I*

Measure	Statistic	Group					
		I T-En	II T-El	III T-En	IV T-El	V UT-En	VI UT-El
Number of 8-in. Maze Sections Traversed	Mean	378.8	15.8	561.4	39.8	401.0	56.4
	s	94.5	25.6	109.8	35.8	147.0	68.1
	Range	291–538	0–61	412–672	7–84	234–633	2–167
Number of Retreats to Cage Rear	Mean			9.8	15.0	12.8	39.2
	s			0.8	2.0	4.2	7.5
	Range			9–11	13–17	8–18	29–49
Number of "Looks Away" from Cage Door	Mean			11.4	29.6	31.4	75.4
	s			4.2	12.2	15.1	10.9
	Range			6–16	13–42	19–56	60–89

* The symbols, T, UT, En, and El denote tamed groups, untamed groups, enclosed-alley groups, and elevated-alley groups respectively; *s* represents the best estimate of the standard deviation.

defined as a nonexposure, following an exposure, of the head receptors to the open cage door when an animal was in the front half of the cage. Criteria for exposure and nonexposure of head receptors to the door proved easy to establish.

Control observations, taken on some of the groups during the 5 min. preceding each trial, revealed that almost all animals were inactive before the cage door was opened. In other words, the base line of intra-cage activity, including "looks" toward and away from the door, was very low.

Results

The measurements taken on each animal were combined for the three days. The results are summarized in Table 1, which shows for each group the mean, standard deviation, and range for each of the three measures.

Number of maze sections traversed. These data are summarized in the upper third of Table 1. The means and ranges reveal that the groups exposed to the enclosed maze (Groups I, III, and V) exhibited a far greater amount of exploratory behavior in the maze than those exposed to the elevated alley. Because there is no overlap in the distributions for the enclosed and elevated groups, tests of significance are unnecessary. A day-by-day analysis yields similar results.

Figure 1 shows the relation between amount of exploratory behavior in the maze and time of exposure for all enclosed and for all elevated groups on each of the three days. These graphs reveal the marked difference in amount of maze behavior that occurred in the two sets of groups. In addition, two aspects of these curves deserve mention. First, on each of the three trials the shape of the curve for the elevated groups is essentially the same, showing a gradual increase in amount of exploratory behavior in the maze over the 10-min. exposure period. The results of a *t* test between the means for the first and last 2-min. periods for all days combined indicate that the rise is real. The value of *t* is 2.94, which is significant beyond the .02 level for 14 *df*. Second, the shape of the curve for the enclosed groups changes markedly over the three trials. On day 1, amount of maze behavior is low initially, increases rapidly to a peak, then decreases. On day 2, it is higher initially than on day 1 and decreases gradually over the exposure period. On day 3, it begins at an even higher level, then decreases according to the negatively accelerated function characteristic of exploratory behavior (e.g., 9, 10). Statistical analyses bear out the above statements. The increase from the first to the third point on the graph for day 1 is significant at about the .02 level (*t* of 2.57; 14 *df*). Mean amount of activity during the first 2-min. period is significantly greater on both day 2 and day 3 than on day 1 beyond the .01 level; the respective values of *t* are 3.67 and 3.11. And, the decrease from the first to the fifth point on the graph for day 3 is significant beyond the .001 level (*t* of 4.15; 14 *df*).

Number of retreats to the rear half of the cage.

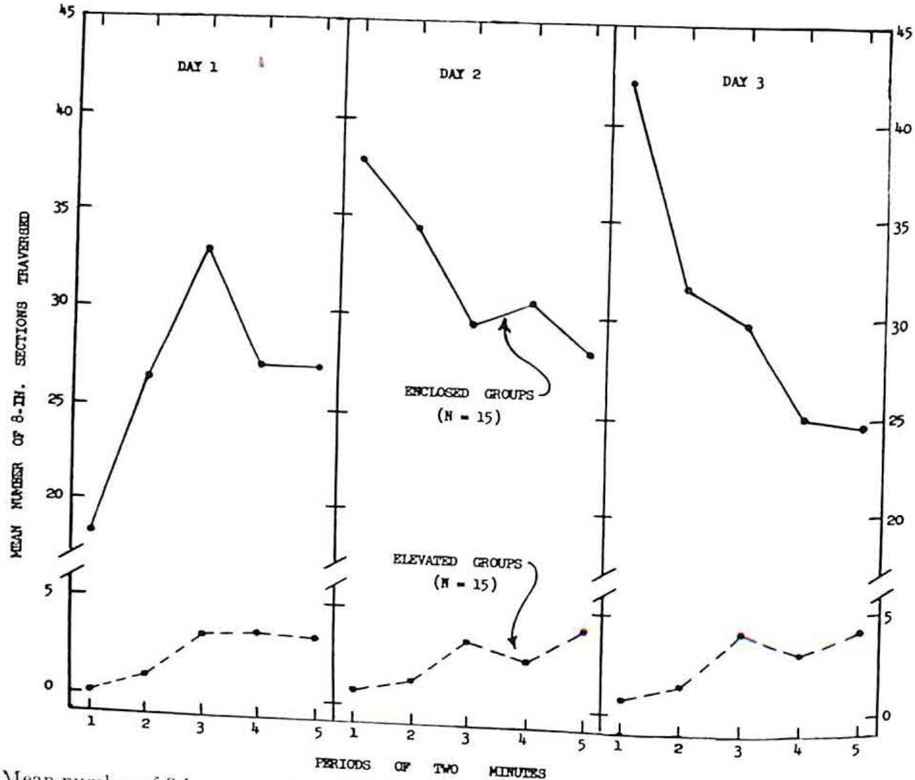

FIG. 1. Mean number of 8-in. maze sections traversed on each day as a function of time. The data are combined for the three enclosed groups and for the three elevated groups.

These data are summarized in the middle third of Table 1. As stated earlier, the rats in Groups III and IV were tamed prior to the experiment whereas those in Groups V and VI were not. Inspection of the table reveals that less avoidance behavior occurred (*a*) in the enclosed than in the elevated groups, and (*b*) in the tamed groups than in the untamed groups. With respect to result *a*: There is no overlap between the distributions for the tamed groups (III and IV) or for the untamed groups (V and VI). In both comparisons, the number of retreats is much greater for the elevated than for the enclosed groups. With respect to result *b*: The distributions for the elevated groups (IV and VI) do not overlap. However, those for the enclosed groups do overlap, and statistical analysis indicates no difference between the means for Groups III and V. Thus, the taming procedure resulted in a decrease in amount of avoidance behavior for the elevated groups but not for the enclosed groups.

Number of "looks away" from the cage door. These data are summarized in the lower third of Table 1. They show that the mean for each enclosed group is much less than that for its corresponding elevated group. The distributions of Groups V and VI do not overlap. However, those of Groups III and IV do overlap; in addition, their variances are not homogeneous. Accordingly, the individual scores for these groups were transformed by taking the common logarithm of each. The variances of the converted scores are homogeneous. A t test performed on the transformed scores yielded a value of 3.01, which is significant beyond the .02 level for 8 *df*. Thus, each enclosed group shows a significantly smaller amount of avoidance behavior than its corresponding elevated group.

Comparison of the means and ranges of the two enclosed groups (III and V) and of the two elevated groups (IV and VI) indicates clearly that the taming procedure resulted in a smaller number of "looks away" from the cage door. There is no overlap in distributions in either of these two comparisons.

Disscussion

The results may be summarized as follows: (*a*) The animals exposed to the enclosed maze exhibited a much greater amount of exploratory behavior in the maze than those exposed to the elevated alley. The ratio is about 12 to 1. (*b*) The elevated-maze rats showed a gradually increasing amount of maze behavior over each 10-min. trial whereas the enclosed-maze animals exhibited an initial increase followed by a decrease on day 1, which changed to a regular, negatively accelerated decrease in amount of maze exploration on day 3. (*c*) The elevated-maze rats showed a much greater amount of avoidance behavior of the maze, as measured by number of retreats to the rear half of the living cage and by number of "looks away" from the open cage door, than the enclosed-alley rats.

The findings bear directly upon the question of whether novel stimulation evokes the fear drive as well as the exploratory drive. First, it is clear that both approach and avoidance behaviors were exhibited by the animals in this experiment whether they were exposed to an enclosed or an elevated maze. This result strongly supports the hypothesis that novel stimulation may evoke the fear drive as well as the exploratory drive. Second, it is evident that the animals exposed to the elevated maze exhibited more avoidance behavior than those exposed to the enclosed alley. The interpretation of this finding is that elevated alleys arouse a greater strength of fear in rats than do enclosed alleys. Third, the findings that the animals exposed to the elevated maze exhibited a greater number of retreats to the cage rear and looks away from the open cage door indicate clearly that the former were subjected to a greater strength of approach-avoidance conflict than the latter. This is so because the measures employed are direct indices of *both* approach and avoidance behavior, e.g., a rat had to enter the front half of a cage before it could retreat to the rear half. These data can be explained in terms of relative drive strength: amount of conflict will increase as the strength of the fear drive increases, providing that the strength of the exploratory drive remains approximately constant. Fourth, the increase in amount of exploratory behavior exhibited by the enclosed animals on trial 1 and by the elevated animals on each of the three trials strongly suggests that the strength of the fear drive decreases with time of exposure to novel stimulation. And fifth, the results for the elevated groups suggest that "spontaneous recovery" of fear occurs when novel stimulation is re-presented after a period of nonexposure. These animals showed a gradual rise in amount of exploratory behavior in the maze on any one trial followed by a drop to near zero at the beginning of the next trial. These systematic changes indicate that fear gradually decreased during each exploratory period but recurred in full strength on the next trial.

The increase over trials in the amount of maze exploration exhibited by the enclosed but not the elevated groups during the first 2 min. of each trial, and the very gradual increase in amount of maze activity shown by the elevated groups on each trial suggest an important generalization: The decrease in strength of fear evoked by novel stimuli is proportional to the amount of *direct contact* with such stimuli. Thus, in the enclosed groups, the strength of initial fear was small enough to permit the rats to begin active exploration of the alley, hence, to extinguish the fear it evoked initially. And, by the third trial these animals began to explore the maze as soon as the home-cage door was opened. On the other hand, in the elevated groups the strength of initial fear was great enough to prevent extensive exploratory behavior with its consequent fear extinction. Hence, these animals, although exhibiting a very gradual increase in amount of maze activity on each trial, were unable to explore the alley actively, partly because of the spontaneous recovery of fear at the beginning of each trial.

EXPERIMENT II

This experiment is designed to determine the effects upon the orderliness of exploratory behavior in a symmetrical Y maze, of varying the number of elevated arms from zero to three, the other arms being enclosed. Its primary purpose is to test in a three-choice situation the hypothesis that novel stimulation evokes both the fear and the exploratory drive by varying the strength of fear. If, as the results

TABLE 2
Summary of Order Analyses for Experiment II*

Group I (En-En-En)			Group II (En-En-El)			Group III (En-El-El)			Group IV (El-El-El)		
Mean Per Cent Choice of Three Successive Unlike Arms											
69.0			38.3			31.3			68.2		
Mean Per Cent Choice of the Same Arm Twice in Succession											
3.8			8.5			20.8			4.9		
Mean Per Cent Choice of Each Arm											
A-En	B-En	C-En	A-En	B-En	C-El	A-En	B-El	C-El	A-El	B-El	C-El
32.8	34.4	32.8	38.6	40.0	21.4	52.6	23.9	23.5	31.4	37.2	31.4

* En denotes an enclosed maze arm, El, an elevated arm.

of the preceding experiment suggest, novel elevated maze alleys evoke more fear than enclosed alleys but about the same strength of the exploratory drive, then the normal pattern of alternation among the three arms of a Y maze should be disrupted in those groups run in mazes comprising both elevated and enclosed arms: the animals should tend to avoid the elevated alleys and explore the enclosed alleys.

Method

Subjects. The *S*s were 24 female albino rats of the Wistar strain. The animals were 80 to 90 days old and experimentally naive. Prior to and during the experiment all rats had free access to both food and water except during the brief experimental sessions.

Apparatus. This consisted of a symmetrical Y maze constructed from unpainted plywood. Each arm could be converted into either an enclosed or an elevated alley. The alleys were 24 in. long and 4 in. wide, and their floors were covered with ½-in. hardware cloth. Enclosed arms were 4 in. high and covered with hinged hardware-cloth tops. The maze was elevated 30 in. from the floor and placed in the center of an 8-ft. square enclosure formed by black curtains. Illumination was provided by a shaded 25-w. bulb suspended 3 ft. above the choice point. The *E* observed the animals in the maze from behind the curtains.

Procedure. After thorough taming, six rats were assigned at random to each of four groups. For Group I the Y maze was composed of three enclosed arms; for Group II, of two enclosed and one elevated arm; for Group III, of one enclosed and two elevated arms; and for Group IV, of three elevated arms. Each animal was given one trial at the same time on each of three successive days. A trial consisted of (*a*) placing a rat in the Y maze at the choice point, (*b*) allowing it to explore the maze freely for a period of 10 min., and (*c*) removing it from the maze. Neither food nor water was ever present in the maze. On each trial a record was made of the sequence of maze arms entered. The criterion for an arm entry was a full body-length entry, excluding the rat's tail, from the choice point of the Y.

Results

Three indices of orderliness of exploratory behavior were computed for each animal for each 10-min. trial: (*a*) The number of triads consisting of entries into three successive *unlike* maze arms, e.g., BAC, was converted into a percentage score based upon the total possible number of such triads. (*b*) The number of diads consisting of re-entry from the choice point of a maze arm just explored without entry into another arm, was converted into a percentage score based upon the total possible number of such diads. (*c*) The number of entries into each maze arm was converted into a percentage score based upon the total number of arm entries, yielding a measure of maze-arm preference. No significant changes in these three indices of orderliness occurred over the three trials. Hence, the data for all three days are combined. The results are summarized in Table 2.

The upper third of Table 2 shows the mean percentage choice of three successive unlike maze arms on all three trials. These data indicate that Groups I and IV do not differ, that Groups II and III do not differ, but that the latter pair of groups exhibits much smaller percentage scores than the former pair. The results of statistical analysis bear out these statements: An analysis of variance performed on these data yields an F ratio of 27.82, a value significant at beyond the .001 level for 3 and 20 *df*. A series of t tests reveal that the means for Groups I and IV do not differ, that the means for Groups II and III do not differ, and that the mean for each of the latter groups is significantly less than the mean for each of the former groups at beyond the .001 level

The middle third of Table 2 shows the mean percentage choice of the same maze arm twice in succession from the choice point. These data indicate that Group III exhibited much more "repeat" behavior than any of the other groups. Statistical analysis substantiates this statement. An analysis of variance of these percentage scores yields an F ratio of 14.58, a value significant at beyond the .001 level for 3 and 20 *df*. A series of t tests shows that the mean for Group III is significantly greater than the mean for any other group at beyond the .01 level, but that no other pair of means differs significantly.

The lower third of Table 2 summarizes the data concerned with maze-arm preferences. Inspection of these data reveals (*a*) that the animals in Groups I and IV distributed their choices equally among the three arms, (*b*) that the rats in Group II entered each enclosed arm approximately twice as often as the elevated arm, and (*c*) that the animals in Group III entered the enclosed arm much more frequently than either of the elevated arms. A series of t tests bears out these statements. No significant difference in percentage of arm entries occurs in Group I or in Group IV. Percentage of entries into each enclosed arm is significantly greater than percentage entry into the elevated arm at beyond the .02 level for Group II. And for Group III percentage of entries into the enclosed arm from the choice point is significantly greater than percentage entry into either of the elevated arms at beyond the .01 level.

Discussion

The results may be summarized as follows: (*a*) The animals exposed to mazes comprising three enclosed or three elevated arms averaged about 69 per cent alternation among the three maze alleys, whereas those exposed to mazes containing one or two elevated arms showed a highly significant decrement in this measure of orderliness, averaging about 35 per cent. (*b*) The rats exposed to the maze containing one enclosed and two elevated arms showed a much greater tendency to re-enter an arm just explored than those in the other groups. In all cases, this was the enclosed arm. (*c*) The animals exposed to mazes comprising three enclosed or three elevated alleys exhibited no arm preferences. However, those exposed to mazes containing one or two elevated arms showed marked preferences for the enclosed alleys.

Previous studies by the senior author (e.g., 9, 10, 11) have shown that when rats are permitted to explore Y mazes comprising either all-enclosed or all-elevated arms, their percentage choice of three successive unlike arms approximates 67. The data of Groups I and IV are in close agreement with this value. The results of these earlier studies also show that the average percentage of arm repeats, i.e., re-entries from the arm just explored from the choice point, approximates five. The corresponding values for Groups I, II, and IV are very close to this value. Finally, these earlier experiments yield little or no evidence for maze-arm preferences. In the present study, the animals in Groups I and IV showed no arm preferences, but those in Groups II and III exhibited preferences for the enclosed arms. Thus, the behavior of Groups II and III of the present experiment differs markedly in its orderliness characteristics from that of Groups I and IV and of animals studied in previous experiments.

The simplest explanation for this change in orderliness of maze behavior is suggested by the results of the preceding experiment: Novel stimulation evokes both the fear and the exploratory drive. The former leads to avoidance behavior; the latter, to approach (exploratory) behavior. Both the elevated and the enclosed arms evoke the exploratory drive, but the former evokes a greater strength of the fear drive than the former. Hence, the animals in Groups II and III tended to avoid the elevated arms and to explore the enclosed arms.

SUMMARY

Two experiments were performed to determine whether novel stimulation evokes both the fear drive and the exploratory drive. In the first experiment 30 rats were given three trials consisting of opening a home-cage door and allowing an animal free access to a maze alley for 10 min.; 15 animals were exposed to an enclosed alley and 15 to an elevated alley. Measures were taken of amount of maze exploration and of approach-avoidance behavior to the entrance of the maze. In the second experiment, 24 rats divided into four groups of 6 each were given three 10-min. trials in a symmetrical Y-maze each arm of which could be made into either an enclosed or an elevated alley. The number of elevated arms was varied from zero to three over the groups. Measures were taken of the orderliness of exploratory behavior.

Four major conclusions are drawn from the results of the two experiments: (*a*) Novel stimulation may evoke both the exploratory drive and the fear drive, thus generating approach-avoidance conflict behavior. (*b*) Elevated maze alleys evoke a greater strength of fear, hence more avoidance behavior, than enclosed alleys. (*c*) The strength of the fear drive evoked by novel stimulation decreases with time of *direct exposure* to that stimulation. (*d*) After a period of nonexposure, re-presentation of novel stimulation results in spontaneous recovery of fear, the magnitude of which depends upon the amount of fear extinguished to that stimulation on previous occasions.

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LEARNING WHEN THE ONSET OF ILLUMINATION IS USED AS REINFORCING STIMULUS

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The concept of reinforcement holds a key explanatory position in several major theories of behavior. Behaviorally, reinforcement is judged to have occurred if (*a*) the reinforcer occurs as a result of, or in close temporal contiguity with, a response of an organism, (*b*) the occurrence of the reinforcer increases the performance strength of the response, and (*c*) occurrence of the reinforcer leads to learning.

On the basis of these criteria, the major classes of events which have been demonstrated to be reinforcers are: (*a*) the presentation of a substance which can reduce an existing need of the organism (food, water, etc.), (*b*) the removal of an aversive stimulus (bright light, electric shock, etc.), (*c*) the presentation of a stimulus which has had prior association with the conditions in *a*, and (*d*) the removal of a stimulus which has had prior association with the conditions in *b*.

These classes of reinforcers have been integrated by Hull (4), in his postulates of primary and secondary reinforcement, under the concept of need reduction. According to this conception, to be a reinforcer an event must either reduce an existing need or have been previously associated with the reduction of an existing need.

A class of events that appears neither to be need-reducing nor previously associated with need reduction has been investigated by Kish and Antonitis (5). They found that such stimuli as microswitch clicks, relay noises, and stimuli produced by a moving platform exerted what appeared to be reinforcing effects on the unconditioned operant behavior of mice. These findings suggested the following hypothesis: A perceptible environmental change, which is unrelated to such need states as hunger and thirst, will reinforce any response that it follows.

The present experiment was designed to provide a direct test of this hypothesis in the light of the criteria for reinforcement presented above. Utilizing the onset of dim illumination as the stimulus to be tested for reinforcing properties, the several possible effects measured were: (*a*) the effect of the introduction of the stimulus as a consequence of a bar-touch response upon the rate of emission of that response, (*b*) the establishment or nonestablishment by such stimulation of learning structures, as evidenced by a significant amount of extinction-responding, and (*c*) the effect upon the response rate of the presentation of this stimulus uncorrelated with the behavior of the subjects.

METHOD

Apparatus

A modified Skinner box was used. It consisted of a cubic experimental compartment of $\frac{1}{4}$-in. plywood with 6- by 6- by 6-in. inside dimensions, a wire-mesh floor, and a removable wooden cover which contained a 6- by 6-in. Plexiglas window. The *Ss* were placed in the compartment by removing this cover. The four walls of the compartment were painted with gray enamel.

A nonmovable U-shaped bar of $\frac{1}{8}$-in. brazing brass protruded into the experimental compartment $1\frac{1}{2}$ in. above the floor and $\frac{3}{4}$ in. from the wall. This bar was insulated from the wall of the box by $\frac{1}{8}$ in. of solid rubber. Contacts with this bar were recorded by means of an electronic contact relay (6). Recording was accomplished with a rigid bar which offered a minimum of perceptible stimulation, other than tactual, to the *Ss* during the recording process.

This experimental compartment was placed within a sound-resisting box, the inside dimensions of which were in inches 14 by 14 by 14, made of $\frac{1}{4}$-in. plywood with 4 in. of Rockwool insulation. Ventilation of this and the experimental compartment was achieved by drawing air through these compartments with a Cenco water aspirator.

Three identical apparatus units were operated simultaneously, and the *Ss* were rotated among these on successive experimental days to counterbalance possible apparatus differences.

Recording equipment consisted of three Mercury 115 VAC 60-cycle counters.

The light stimulus was provided by a frosted $7\frac{1}{2}$-w.

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GE bulb operating at 115 VAC. This bulb was placed in a wooden lampshade 6 by 6 by 5 in. which fitted in the cover of the experimental compartment. The intensity of the light was reduced by filtering it through three sheets of white mimeograph paper. The light circuit was operated through the relay of the electronic circuit. Each closure of the relay activated the light and recorder circuits simultaneously. Both light and recorder circuits were so designed that they remained closed as long as contact with the bar was maintained. No other source of illumination was provided. The animals were in total darkness at all times except when the light stimulus was presented. The light stimulus could also be presented for $\frac{1}{2}$ sec. at a number of different time intervals by means of a timing device which was incorporated into the circuit.

Subjects

The *S*s were 16 experimentally naive female C57 Black Subline 10 mice approximately 56 days of age at the beginning of experimentation.

The mice were individually housed in the standard wooden boxes in use at the Jackson Laboratory and had free access to food and water at all times except during the 25-min. testing period. The laboratory was lighted from 9 A.M. to 5 P.M. During this period, once each week, the food hoppers and water bottles were refilled. This was done while food and water still remained from the previous filling.

Procedure

Phase 1—habituation. Since preliminary experiments seemed to indicate that the effects of introduction of the stimulus were enhanced by an habituation period, days 1 through 7 were devoted to an operant level determination and habituation to the experimental compartment. All 16 *S*s were run for 25 min. per day in total darkness. Touches upon the bar were recorded but did not result in the onset of illumination. The animals were then divided into two groups of eight mice each, the groups equated on the basis of mean total numbers of responses emitted during days 5, 6, and 7.

Phase 2—conditioning. On day 8, the *S*s of the experimental group (stimulus group) received the onset of illumination as the consequence of each bar contact. The *S*s of the control group (nonstimulus group) continued as in phase 1.

Phase 3—extinction. On days 9 through 12, all *S*s were tested under the conditions of phase 1.

Phase 4—uncorrelated stimulation. On day 13, the control group received 150 $\frac{1}{2}$-sec. presentations of light at 10-sec. intervals. The light flashes were not correlated with the behavior of the *S*s. The experimental group continued as in phases 1 and 3.

Total number of bar contacts during each 25-min. experimental period was recorded for each *S*.

RESULTS

The results are presented graphically in Figure 1. The graph shows the mean numbers of bar touches emitted by the stimulus and nonstimulus groups during each of the 13 experimental sessions. It is apparent that the two groups were well matched since the group means differed but slightly during the seven days of the habituation period.

On day 8, the mean number of responses emitted by the stimulus group is more than twice that emitted by this group on day 7. The resulting difference between the stimulus and nonstimulus groups on day 8 is significant beyond the .005 level for a two-tailed t test ($t = 4.14$, $df = 8$). An F test for homogeneity of variance between the two groups on day 8 showed that the stimulus group was significantly more variable than the nonstimulus group ($F = 19$, $df = 7, 7$, $p < .01$). For this reason the t test used above is an approximate test indicated for use when the assumption of homogeneity of variance cannot be met (1, p. 105).

During the four extinction days, the mean number of responses emitted by the stimulus group remained greater than that of the nonstimulus group, but the difference between the two groups decreased over the four days. On day 9 the difference was still significant at the .005 level ($t = 3.06$, $df = 14$). On day 10 the difference was not significant ($t = 1.98$, $df = 14$, $p = .10$). On day 11, due to an increase in the responses emitted by the stimulus group, the difference approached significance ($t = 2.11$, $df = 14$, $p > .05$). The difference on day 12 was extremely small and not statistically significant. The variance of the two groups was found to be homogeneous throughout the extinction period.

On day 13 the mean number of responses emitted by the nonstimulus group increased slightly over day 12. This increase presumably is due to the presentation of 150 light flashes which were uncorrelated with the behavior of the *S*s. This increase from day 12 to 13 results in a t value of .80 which is not significant. Analysis of the data of individual *S*s in this group on day 13 revealed that this increase in mean number of responses was primarily contributed by three animals whose initial response rates were high. With *S*s having high response rates, chance correlations of responses and light flashes become more probable.

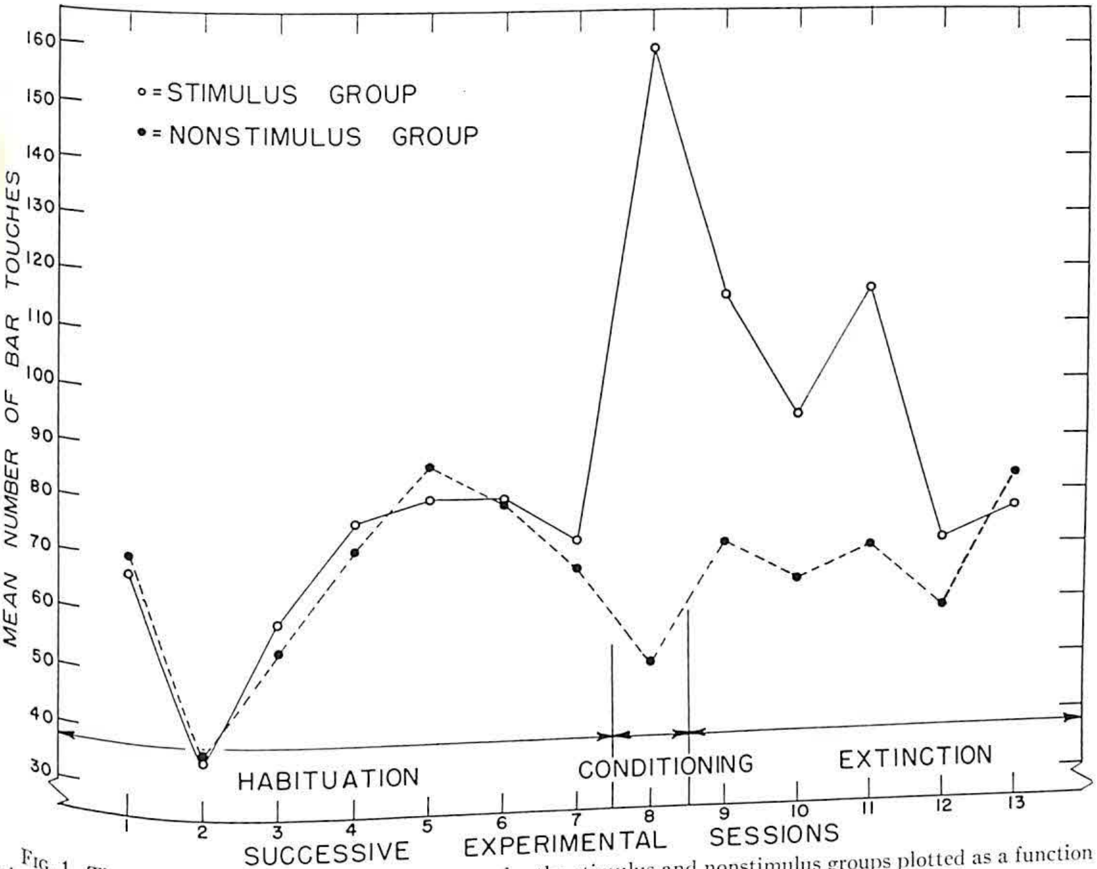

FIG. 1. The mean number of bar-touch responses for the stimulus and nonstimulus groups plotted as a function of successive 25-min. experimental sessions.

DISCUSSION

The data clearly demonstrate that the onset of dim illumination occurring as the consequence of a response, leads to behavioral effects which correspond to those noted as the criteria for the occurrence of reinforcement. The onset of illumination when presented as the direct consequence of a bar-touching response produced a marked and significant increase in the bar-touching rate. Furthermore, a significant amount of extinction-responding was demonstrated as an aftereffect of exposure to such stimulation. These results, therefore, appear to support the hypothesis that a perceptible environmental change, which is unrelated to such need states as hunger and thirst, will reinforce any response which it follows. Several problems, however, are raised by the statement of the hypothesis in such a general form.

1. No restrictions, other than perceptibility, are placed upon the modality which the environmental change must stimulate in order to function in a reinforcing manner. Thus, light onset is assumed to be representative of stimulation in other sense modalities. Some evidence can be marshalled in favor of this assumption from published experiments which utilize stimuli in various sense modalities and which report results similar to those reported here. Sharpe (7), using the sound of a chime as the reinforcer, reported significant increments in the chain-pulling rate of preschool children. In a situation similar to that of the present experiment, Girdner (2) reported increases in the bar-touching rate by rats when each response was reinforced by either the appearance of a dim spot of light above the animal or the onset of a buzzer noise.

2. Phase 4 of the present experiment was included as a test of an alternative to the conditioning-reinforcement interpretation. According to this alternative interpretation, the increase in bar-touching rate was not the result

of a direct reinforcement of that response, but the reflection of an increase in general activity resulting from stimulation by the repeated onset of light. This hypothesis was tested by presenting the onset of light uncorrelated with any specific response of the *S* and measuring the specific response of bar-touching. Since the effect of this procedure was not significant, the activity-increase interpretation does not appear to account for the present findings.

3. The hypothesis does not specify whether the process involved here is one of primary or secondary reinforcement. Several considerations, however, would appear to indicate that this process is not one of secondary reinforcement. The *S*s were given no training associating the onset of light with primary reinforcement. Organic drives were kept at minimal strength by allowing the *S*s free access to food and water at all times except for the 25-min. experimental period. Furthermore, the nocturnal habits of the mouse would make the association of primary reinforcement and light less probable than such an association with darkness.

Apparently, the process involved in this experiment is that of primary reinforcement. The term, in this case, is used in its broadest sense as referring to a process for the operation of which a minimum of previous learning is necessary. The term is not used here to denote the process defined by Hull (4) as involving the reduction of a need. Such usage with reference to the present phenomenon appears to be decidedly premature. In the present study, at least, there is no evidence for any drive or need that could be reduced by the onset of light.

Such a drive, however, has been postulated. Harlow (3) has integrated the results of a number of studies, similar to the present one, under the concept of exploratory drive. It is conceivable that the onset of light in the present experiment was acting as a reinforcer with respect to an exploratory or curiosity motive. Behavioral data of the type presented here, however, do not constitute sufficient evidence for a demonstration of the operation of a drive. Such evidence might be offered by experiments in which the reinforcer is held constant and the influence of other nonstimulus variables, such as deprivation from stimulation, upon the magnitude of the reinforcement effects is studied.

SUMMARY

Two groups of eight female C57 Black 10 mice each were tested in a modified Skinner box to examine the hypothesis that: A perceptible environmental change which is unrelated to such need states as hunger and thirst will reinforce any response which it follows. The effect, upon the emission rate of a bar-contact response, of the onset of dim illumination which followed this response was tested.

Introduction of the stimulus significantly increased the rate of emission of this response. Significant extinction effects were also noted when stimulation was discontinued. The results were considered to be in agreement with the initial hypothesis and were discussed with reference to the general implications of the hypothesis.

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ACTIVITY AS A FUNCTION OF A RESTRICTED DRINKING SCHEDULE

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Two studies (4, 5) indicated that when albino rats were on a restricted feeding schedule (23-hr. deprivation, 1-hr. feeding), their activity increased as a negatively accelerated function of the number of days of restricted feeding. These results seemed to question the implicit assumption in many learning experiments employing food deprivation as a source of motivation that equal, daily periods of deprivation do not result in a systematic change in drive strength. In view of the use of water deprivation as a common source of motivation for rats, it seemed important to extend the results of the previous investigations into this area.

METHOD

Subjects

The *S*s were 24 male Sprague-Dawley albino rats, aged 90 to 100 days at the beginning of the experiment. One *S* was eliminated from the study for failure to run. Of the remaining 23, 16 comprised the experimental group and 7 the control group.

Apparatus and Procedure

The procedure has been described previously (4); therefore, only a brief outline will be presented. The number of activity wheels available necessitated running the study in two consecutive sessions in order to provide a suitable *N*. Ten wheels were available during Session I; 14 were available during Session II. The wheels were the standard Wahmann activity drums equated for frictional torque by the method of Lacey (6). The drums were located in a light-tight room and upon a macadamized floor. Room temperature throughout the experimental period was recorded continuously with a thermograph. The temperature averaged 72°F. with a range of 70° to 74°. Daily fluctuations rarely exceeded 1°.

Session I originated with 5 experimental and 5 control *S*s. One control *S* was eliminated because its record during the base week indicated an average of just two revolutions per day. Session II originated with 11 experimental and 3 control *S*s. Two considerations prompted this unequal distribution of *S*s: (*a*) the desire to provide as large an experimental group as possible, and (*b*) five previous sessions utilizing the same procedure and environmental conditions had indicated that the control *S*s' behavior in this situation was a very stable phenomenon.

The *S*s were placed in the wheels and given an *adaptation period* of 14 days. Food and water were continuously available during this period. Immediately following the adaptation period, the *base period* began. This consisted of a 7-day period in which the room was isolated and darkened except for daily 1-hr. periods under full illumination. During this time, counter readings were taken and food and water replenished. Food and water were continuously available during the base period. The *experimental period* immediately followed the base period and continued for 21 days. The control *S*s continued on the base period regimen. The experimental *S*s were placed on a restricted drinking schedule and permitted access to water only from 11 A.M. until 12 M. each day. Food was continuously available during this period.

RESULTS AND DISCUSSION

Each *S*'s base rate (in revolutions per day) was obtained by totaling the number of recorded revolutions during the 7-day base period and dividing by 7. The *S*'s activity for each experimental day was divided by the base rate in order to obtain a daily figure expressed in terms of a percentage of the base rate. The mean daily activity for the control *S*s for the 21-day experimental period was 110.3. The mean daily activity for the experimental *S*s for the same period was 165.0.

The large difference between the variances of the experimental and control groups necessitated the use of the Festinger technique (2). Each *S*'s daily running activity, in percentage of base rate, was totaled and a mean obtained for the 21-day period. Appropriate rankings based on these means were then given to the experimental and control *S*s. Results indicated that the difference between the experimental and control groups was significant beyond the .05 level of confidence.

The means for the experimental and control *S*s for each day of the experimental period are indicated in Figure 1 along with the combined results of two previous studies (4, 5) in which the same environmental conditions prevailed and the same procedure was followed except that food rather than water deprivation was utilized. Inspection of the plots indicates the stable control curve, a little above the expected level of 100 per cent. The activity for the water-deprived group is also surprisingly stable, although somewhat higher than that of the control group. This latter level of activity is in sharp contrast to the activity exhibited by the food-deprived animals. The progressive increase in activity which tends to accompany

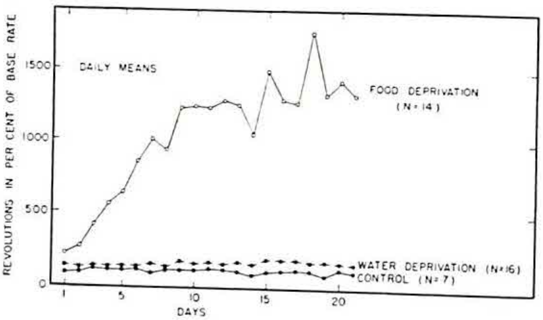

FIG. 1. Running activity, in percentage of base rate, for the 21-day experimental period.

the restricted feeding schedule is not characteristic of animals placed on a water deprivation schedule.

If the level of activity is assumed to be a valid index of the strength of motivation, two conclusions may be drawn from the findings. First, a restricted feeding schedule results in considerably greater motivational strength than a restricted drinking schedule. This finding is not in agreement with the common assumption that lack of water results in *greater* motivation than lack of food.[1] It is important, of course, to keep in mind the well-known interrelationship between food and water ingestion. Rats deprived of water do not eat as much food as usual, and rats deprived of food do not drink as much water. Thus, the present experimental findings do not represent a comparison between a pure hunger and a pure thirst drive.

The second conclusion to be drawn is that a prolonged period of restricted drinking seems less likely to result in a progressive increase in motivational strength than a similar period of restricted feeding. Thus, from a methodological standpoint, water deprivation would seem to be superior to food deprivation as a source of motivation. Unfortunately, an explanation for such a fundamental difference between the operation of the two drives is not immediately apparent.

Campbell and Sheffield (1) have stated that there should be "little change in activity in an animal in a drive state unless there were some external stimulation." In the present study, the light-tight room excluded the possibility of the animals' receiving visual stimulation for 23 hr. of each day. Inasmuch as the experimental animals' time was devoted primarily to drinking and eating during the twenty-fourth hour, when illumination was present, the animals' total daily running activity is reflected in the 23-hr. period in which there was no visual stimulation. Although sound stimulation was not eliminated, previous work (5) has indicated that deafened animals, run under conditions of either satiation or food deprivation, show as much activity as animals which are permitted to hear the usual sounds present in the experimental situation. Thus, the present study supports a previous one in demonstrating that although external stimulation is minimized, an increase in the drive state (hunger or thirst) *does* result in an increase in activity. It is difficult to reconcile such experimental evidence with the Campbell-Sheffield hypothesis.

SUMMARY

The present study was an attempt to determine the activity level of albino rats placed on a prolonged period of restricted drinking. Seven control animals were given free access to food and water; 16 experimental animals were given free access to food but 23-hr.-per-day water deprivation for a period of 21 days. The mean daily activity of the experimental group was significantly higher than that of the control group; however, no progressive increase in activity such as has been found with food deprivation was observed over the 21-day experimental period.

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[1] It should be noted that Finger and Reid (3) have also questioned this assumption.

FOOD INTAKE IN THE RAT AS A FUNCTION OF DEPRIVATION INTERVALS AND FEEDING RHYTHMS[1]

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Studies of the relationship between food deprivation and measures of drive make use of two conflicting concepts. It is usually assumed that drive is an increasing monotonic function of the number of hours of food deprivation, at least within limits. At the same time hunger is spoken of as a rhythmic phenomenon as though the tendency to eat, and by implication the drive, reaches a maximum at periodic intervals and then subsides. This latter possibility suggests that a simple increasing relationship between deprivation and drive would exist only from the beginning of a deprivation interval to the maximum point, and that, with longer deprivation intervals, measures of drive would show a decrease.

The present study investigates the relationship between an established eating rhythm and the amount of food ingested after varying intervals of deprivation. Thus, it is dealing with consumatory behavior rather than instrumental behavior, the usual measure of drive level. In addition, it compares the eating behavior of a periodic group with a second group whose eating experience had always been of an aperiodic, nonrhythmic nature.

METHOD

Thirty albino rats of the Slonaker strain, approximately 120 days of age, were used. Half were males and half were females. From birth these *S*s had been raised in group cages with access to food and water at all times.

The experiment was conducted in a soundproof room with the temperature maintained between 73° and 77° F. The room lights were left on. Consequently the only external cue indicative of a day-night cycle was the presence of *E* at odd times between 9 A.M. and midnight.

The *S*s were maintained in individual cages 8 by 8 by 12 in. A 2-in. hole in the front wall gave access to the food tray. The food consisted of small Purina Frisky pellets. By covering the food pan with ½-in. wire mesh *S* was forced to pick out the individual pellets with its front paws. This reduced spillage of food to a minimum. However, a metal pan was placed under each cage to facilitate the recovery of any pellets that dropped through the mesh floor of the cage.

While adapting to the experimental situation during the first four days, the *S*s had continuous access to food and water. They were then divided into two groups matched for weight and food intake during the previous two days. The Periodic Group (P) consisted of 20 *S*s, half male and half female. The remaining 5 males and 5 females were assigned to the Aperiodic Group (A). Both groups were then placed upon a pretesting deprivation schedule.

In order to facilitate the testing procedure that came later, the P group was divided into four subgroups (P-1, P-2, P-3, and P-4), approximately matched for weight and intake, and each containing either three males and two females or two males and three females. Starting on the fifth day, these four subgroups had access to water at all times but had food available for only 3 hr. each day. The schedule of feeding was as follows: P-1 from 900 to 1200, P-2, from 1300 to 1600, P-3 from 1700 to 2000, and P-4 from 2100 to 2400. This schedule was continued for 27 days in an attempt to establish a 24-hr. feeding rhythm. The *S*s were weighed to the nearest gram each day before the feeding period, and their food intake, allowing for spillage, was measured to the nearest tenth of a gram.

The A group was placed on a highly variable deprivation schedule to prevent a definite feeding rhythm from being established and at the same time to acquaint the *S*s with a wide variety of deprivation intervals. All food was taken from them at 900 on the fifth day. Counting hours from the beginning of one feeding to the start of the following one, the sequence of intervals between feedings was as follows: 48, 4, 44, 12, 24, 40, 20, 32, 16, 28, 8, and 36. These 12 intervals were then repeated in the order: 8, 44, 20, 48, 4, 32, 24, 16, 28, 40, 36, and 12. Food was available for 3 hr. at each feeding. The *S*s were weighed each day at 900 and their food intake measured at the end of each feeding.

Starting with day 28, a new regime of test feedings was introduced. All *S*s in the P groups were fed at their usual time on this day, those of the A group at 900. Then the four P subgroups were tested at 8 of the 12 deprivation intervals listed in Table 1. Each subgroup was tested on a different set of 8. This arrangement permitted all testing to be done between 900 and 2400 each day. At the same time it was possible to have 10 or more *S*s sampled for each of the 12 deprivation intervals. Food was available for 3 hr. at each test feeding.

To maintain the rhythm of the P subgroups during this testing, the procedure illustrated at the bottom of Table 1 was employed. After being fed at its regular time of 900 on day 28, *S* was placed on its first deprivation interval of 8 hr. and then given its first test feeding at 1700 on the same day. The following day it was again fed at its usual time of 900, placed on a

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[1] This study was supported in part by a research grant from the Nutrition Foundation of New York.

[2] Now at the University of Wisconsin.

TABLE 1

Deprivation Intervals for the Periodic Subgroups

Subgroup	Regular Time	4	8	12	16	20	24	28	32	36	40	44	48
P-1	900	X	X	X			X	X	X	X			X
P-2	1300	X	X			X	X	X	X			X	X
P-3	1700	X			X	X	X	X			X	X	X
P-4	2100			X	X	X	X			X	X	X	X

Illustrative Schedule for One P1 Animal

Day	1	2	3	4	5	6	7	8	9	10	11	12	13
Reg. Time	900	900	900	900	—	900	—	900	—	—	—	900	—
Test Time	1700	2100	1300	—	1300	—	1700	—	900	—	900	—	2100
Deprivation Interval	8	12	4	—	28	—	32	—	24	—	48	—	36

deprivation interval of 12 hr., and then given a test feeding at 2100. It was fed again at 900 on the third day. Thus a regular feeding at 900 intervened between each pair of test feedings. The exception to this rule was after a 24-hr. deprivation interval; as this test feeding came at the regular feeding time, a second deprivation interval was started immediately. It should be noted that the test feedings, except for the 24- and 48-hr. deprivation intervals, came at times in the day such that *S* had not previously experienced them as feeding periods. Each of the 20 *S*s in the P group went through the eight deprivation intervals in a different order. As far as possible these orders were arranged so that each deprivation interval occurred equally frequently at each testing so as to allow for any progressive change in intake during this time.

The *S*s in the A group were tested at each of the 12 deprivation intervals listed in Table 1, one test following the other without any intervening feeding period. Food was available for 3 hr. at each test. A different order of intervals was used for each *S* to allow for progressive changes in intake, but these orders were so restricted that all testing could be done between 900 and 2400. Having completed a cycle of such tests, each *S* immediately started a second cycle but with a different order of intervals. All *S*s of Groups P and A were weighed each day at their regular time. Their food intake at each 3-hr. feeding, whether regular or test, was measured to the nearest tenth of a gram.

Because of the possibility of interactions between successive deprivation intervals with repeated testing of the same *S*, all *S*s in the P group were given a post-test series using a more conventional design. The four deprivation intervals of 12, 24, 36, and 48 hr. were used. Immediately following the test series all *S*s were returned to their regular feeding period for three days. Next, each *S* was tested at one of the above intervals, then returned to the regular feeding schedule for three days, next tested at a different interval, and so on. Thus, three days of feeding at the regular time intervened between each test. Each *S* went through the four tests in a different order.

RESULTS

The matching of the four periodic subgroups was checked by two analyses of variance: one on their weight, and the other on their food intake for the five days preceding the first test feeding. In neither instance did the differences between groups or between days reach the .05 level of significance. This suggests that the four groups were adequately matched for weight and intake and that these variables had stabilized during the pretest period.

The legitimacy of averaging the test data from the four groups was checked by another analysis of variance. All these *S*s had been tested after 24 and 48 hr. of deprivation. Consequently, the equality of reaction of these four groups to the deprivation intervals was judged from these two test scores for each *S*. The results are shown in Table 2. There is no indication of any significant difference between groups, but there is a highly significant difference between the 24- and 48-hr. intervals. The mean intake for these two intervals is 9.63 and 7.82 gm., respectively, indicating that the *S*s ate considerably less after 48 hr. of deprivation than after 24 hr. On the basis of the above analysis it appeared legitimate to average the test data from the various subgroups.

The solid line in Figure 1 indicates the relationship between average intake and length of deprivation when the *S*s have had previous experience with a 24-hr. feeding schedule. It should be noted that the curve rises to a maximum after 24 hr. of deprivation and falls off at longer deprivation intervals. There is no

TABLE 2

Analysis of Variance of Intake at 24- and 48-hr. Deprivation Intervals for Periodic Subgroups

Component	*df*	Variance
1. Subgroups	3	1.06
2. Deprivation Intervals	1	32.76*
3. Interaction (1 × 2)	3	4.03
4. Animals within Subgroups	16	5.09
5. Interaction (2 × 4)	16	3.21

* Significant at .01 level.

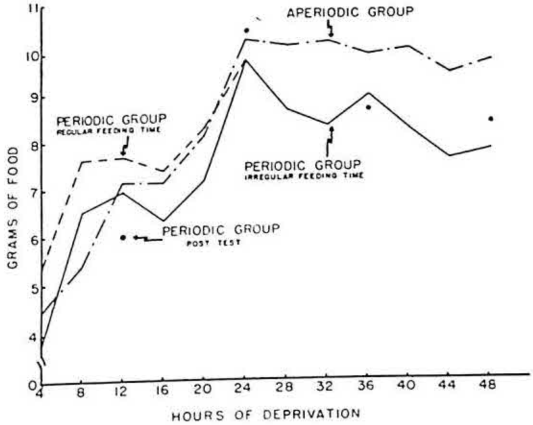

FIG. 1. The solid curve represents the average food intake during a 3-hr. period after varying intervals of deprivation for a group of animals in which a 24-hr. hunger rhythm had been established. The dot-dash line is the same relationship for a group that had previously been fed at irregular intervals. The broken line is based on the first group when the test feeding occurred at the same time of day as had the regular feeding during the establishment of the hunger rhythm.

evidence of a second increase at 48 hr. even though this test feeding occurs at the same time of day as the regular feeding period.

The solid circles in Figure 1 indicate the average intakes of these *S*s after 12, 24, 36, and 48 hr. of deprivation as measured during the posttest series. Their close agreement with the solid line indicates that the same general function is obtained under two quite different methods of testing.

The fact that the *S*s in the P group were given a regular feeding before each test feeding makes it possible to derive a second function relating average intake to hours of deprivation, at least over the range from 4 to 24 hr. This function is based on the deprivation intervals from the beginning of a test feeding to the beginning of the next regular feeding. The contribution of each *S* to this function can be computed from Table 1 by considering the differences between 24 or 48 hr. and each test interval indicated there. This relationship is indicated by the broken line in Figure 1. In each instance the average intake per deprivation interval is greater on this curve than for the previous test data. This suggests that for a given deprivation interval an *S* will eat more if the feeding comes at its regularly scheduled time of day than if it comes at a time of day it has not previously experienced. No attempt was made to determine the significance of this difference because of the complex intercorrelations between the two sets of data.

The relationship between hours of deprivation and average intake for the aperiodic group is shown by the dot-dash line in Figure 1. This is based on the combined data for the two replications with this group. The legitimacy of this combining of data was established by an analysis of variance. Neither the mean difference in average intake between the two replications nor the interaction between replication and hours of deprivation were significant at the .05 level of significance. This curve indicates that the relationship between average hours of deprivation and intake is very similar for the A and P groups for intervals between 4 and 24 hr. For longer deprivation intervals, however, the average intakes of the two groups differ markedly. As indicated previously, the P group ate significantly less after 48 hr. than it did after 24 hr. A similar analysis of the A data fails to show any significant drop in intake over this interval.

Because of this marked difference in eating patterns, a check was made of the equality of the two groups with respect to weight. For the interval including the five days prior to testing and the entire test period, the P group averaged 210.0 gm. and the A group 203.3 gm. The difference was small but statistically reliable. The P group showed no average change in weight during this period whereas the A group showed a gradual but significant loss, and probably resulted from the fact that during the testing the P group, as the result of the combined test and regular feedings, averaged 14 feedings in 13 days whereas the A group had only 12 feedings. This is also mirrored in the average daily intake of the two groups during the test period; the P group averaged 8.61 gm. and the A group, 7.76 gm.

DISCUSSION

In interpreting these results it should be borne in mind that the previous eating behavior of these *S*s had not been controlled. While raised in group cages with food and water always present, it is highly probable that all animals had established a day-night rhythm of eating and had experienced either self-imposed or accidentally imposed deprivation intervals of varying lengths. This type of experience would tend to obscure the influence of the experimentally imposed eating rhythm. The fact, however, that the four subgroups among the periodic animals showed no differences in average intake at the end of the pretest period, even though they were fed at different times throughout the day, suggests that the experimentally established rhythm had overridden any previous day-night cycle of eating activity. Furthermore, the repeated testing of each *S* may have been a complicating factor, but the fact that the posttest gave the same results tends to rule this out as an important variable.

The difference in eating behavior of the periodic and aperiodic groups in this study supports the idea that the amount an *S* eats after a given deprivation interval is in large part a function of previous experience. The increase in intake in both groups up to 24 hr. of deprivation could readily be explained as a concomitant of digestive and metabolic processes. But the fact that with longer deprivations the periodic group shows a decrease, whereas the aperiodic group does not, implies that this difference is a function of their differential experience with various feeding intervals. The periodic group probably had never experienced intervals of deprivation as long as 36 or 48 hr. Consequently, the decrease in amount eaten at these longer intervals can be readily accounted for by stimulus generalization or by similar concepts (1). It has previously been shown that when a deprivation interval is introduced for the first time, rats tend to eat very little and only gradually increase their intake with repeated experience with this interval (2). This finding can be generalized to the present study only with caution, however, because it involved simultaneous changes in weight which were not characteristic of the present experiment.

The fact that the intake of the aperiodic group leveled off after 24 hr. deprivation is primarily due to the length of the feeding period used. It was observed that all *S*s did most of their eating in the first hour and then tended to sleep during the remaining 2 hr. although occasionally returning for a few more pieces of food. It would appear that an average of 10 to 11 gm. of food was the maximum these *S*s could eat during one continuous feeding under the conditions of this experiment.

The relationship between intake and deprivation seems to be further complicated by the time of day at which the test feeding is given, once a rhythm has been established. Figure 1 indicates that the periodic *S*s tended to eat more for a given deprivation interval if the feeding came at the regularly established time of day than if it came at a relatively unfamiliar time. The fact that the external environment was relatively constant in this study throughout the 24 hr. would suggest that this was the result of some internal state of the animal. But the role of external cues, such as the presence of *E*, can not be ruled out completely.

The interpretation of this difference is further complicated by the fact that in this study the deprivation interval preceding a regular feeding is negatively correlated with the deprivation interval preceding the prior feeding at an irregular interval. For instance, if, after a regular feeding, an *S* was given 20 hr. of deprivation and then a test feeding at an irregular time, this was immediately followed by a feeding at the regular time after only 4 hr. of deprivation. How this would account for the difference in intake measures after a constant deprivation interval is not clear. In any event, this difference complicates a simple stimulus generalization account of the curve for the periodic group.

A final point of interest is the absence of any indication of a second maximum in intake at 48 hr. of deprivation even though this test feeding always came at the regular time of the day. It tends to rule against an explanation of these results in terms of an "internal clock" or other rhythmic mechanism independent of learning.

SUMMARY

Thirty albino rats were divided into two groups, a periodic and an aperiodic feeding group. For 27 days the periodic group was fed for 3 hr. each day at the same time in order to establish an eating rhythm. During this time the aperiodic group was fed for 3 hr. at a time, but the deprivation interval between feedings varied from 4 to 48 hr. in irregular succession. Both groups were then tested with respect to food intake after varying intervals of deprivation ranging from 4 to 48 hr.

1. Both groups showed an increase in the amount eaten with increasing intervals of deprivation up to 24 hr. With longer intervals the periodic group showed a decrease whereas the aperiodic group showed no change.

2. For a given deprivation interval, the periodic group tended to take in more food if the test feeding came at the regularly scheduled time of day than if it came at any other time.

3. There was no evidence of a second maximum in intake at 48 hr. of deprivation for the periodic group even though this test feeding always came at the regularly scheduled time of day.

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DOES THE ACTIVITY WHEEL MEASURE GOAL-STRIVING?[1]

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In addition to drives resulting from tissue needs, reference can be found in the experimental literature to a motivational construct more closely related to goals. Hull's (5) Postulate VII defines "incentive motivation." What Tolman used to call "appetite" (13) he now calls "cathexis" (14). Maltzman (8) suggests the term "process need" for this variable. The senior author (11) has used "tertiary drive" for the same purpose. Underlying all these terms is the notion that the partial arousal of a consummatory response has an energizing effect on behavior, an effect here referred to as *goal striving*.

To confirm this hypothesis and to determine its conditions, without invoking secondary reinforcement, it is desirable to have a measure independent of any instrumental response. Geier (3) and Geier and Tolman (4) used the activity wheel to provide such a measure. In the first study Geier found that hungry rats confined in a wheel for 1 min. turned it more often when fed immediately afterward than when not. In the second study, by confining rats in a series of wheels placed at regular intervals across a runway to food, the authors demonstrated a goal gradient of wheel-turning. The measure therefore seemed ideally suited to further study of goal-striving.

In a first attempt, after adaptation to activity wheels and to the apparatus, 16 rats were trained to discriminate, as shown by running times, between two alleys painted with crosswise and lengthwise black and white stripes. One alley led to food, the other did not. We then inserted an activity wheel halfway down both runways and compared the numbers of revolutions in 1 min. of confinement. No difference appeared. But since the discrimination broke down at the same time, the result was not crucial either for the goal-striving hypothesis or for the measure used.

Before revising the experimental design, however, we thought it advisable to validate the measure by repeating the essentials of Geier's technique.

EXPERIMENT I

Method

The apparatus consisted of an activity wheel 14 in. in diameter at right angles to an alley 12 in. long. At the other end of the alley an opening on one side gave access to a wooden box 10 by 10 by 10 in., invisible from the wheel. There were two sliding doors on opposite sides of the wheel: through one the rat was inserted; the other gave access to the alley. Originally transparent, halfway through the matching trials these doors were made opaque in order to reduce distraction.

Subjects. Fourteen male hooded rats, 2½ mo. old at the outset, were housed in individual cages attached to activity wheels throughout the experiment. Water was always available.[2] Once a day just after the time of experimenting they were fed Steenbock mash and Rockland pellets for 1 hr. in group cages.

Adaptation (10 days). Five days were allowed the *S*s to become accustomed to running the wheels attached to their cages. On day 6 *S*s explored the apparatus for 10 min. in groups of three or four. On day 7 they explored it singly for 5 min. On days 8 to 10 two trials a day were run to habituate the *S*s to confinement in the wheel. Starting with the exit door open, *E* kept it closed on succeeding trials 0, 5, 10, 20, and 30 sec. before releasing *S* into alley and endbox.

Matching trials (12 days). Two trials a day were given, spaced about 45 min. apart. After 45 sec. of confinement the wheel was stopped by hand and the exit door opened. The *S* was removed 30 sec. after entering the endbox.

On the basis of total revolutions during these trials 12 *S*s were matched and assigned at random within pairs to Groups E and C. Two *S*s were discarded.

Test trials (19 days). Subjects were run in a random order, varying from day to day. Group E found mash in a glass furniture coaster in the endbox; Group C found an empty coaster. Besides number of revolutions, *exit time* was taken manually; this measure is defined as the time from opening the exit door until *S* entered the endbox.

During the test series certain modifications were introduced as follows:

Days 1 to 5. Three trials a day were given at 40-min. intervals. The wheel was stopped after 45 sec., but the exit door was not opened until 60 sec. This was done to prevent possible reinforcement of wheel-turning by immediate eating. Both groups were removed 30 sec. after entering the endbox.

Days 6 to 19. Since Geier may have used massed

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[1] Aided by a grant from the Committee on Research, University of California.

[2] Since only 12 wheels were available, two plain cages were also used, and one pair of *S*s was rotated among the wheels; all *S*s therefore spent six days out of seven in activity cages until the end of matching trials, when two *S*s were discarded.

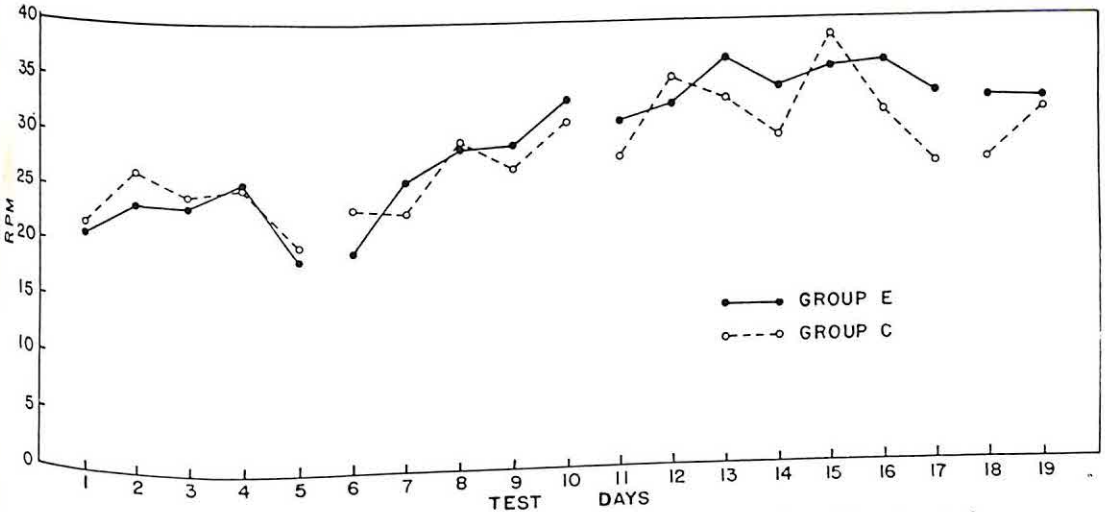

FIG. 1. Mean revolutions per minute for Groups E and C on test days (Experiment I).

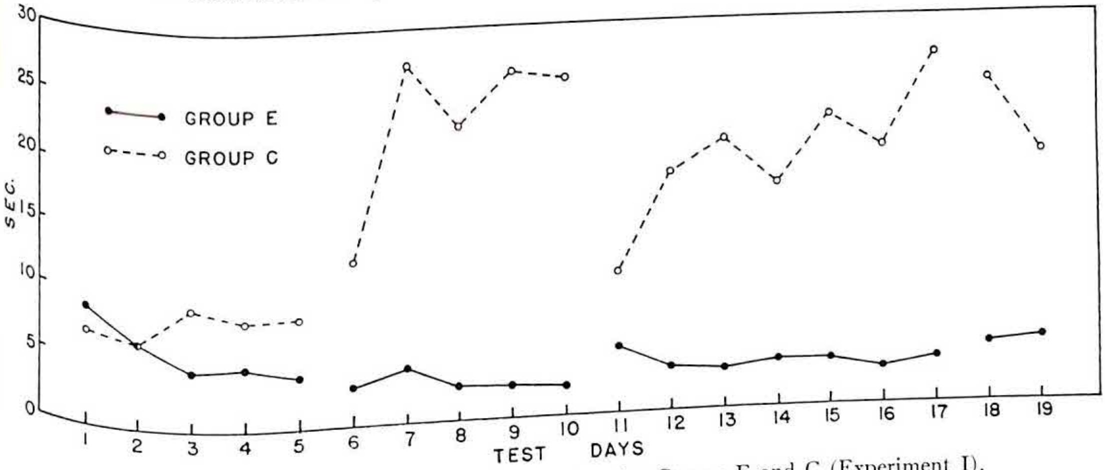

FIG. 2. Means of median exit times on test days for Groups E and C (Experiment I).

trials, although he was not explicit on the point, we gave four massed trials a day for the rest of the series.

Days 11 to 19. In a further attempt to copy Geier's conditions more closely and to test the possible role of reinforcement, *E* stopped the wheel and opened the door simultaneously at 60 sec.

Days 18 to 19. Duplicating Geier's technique in one more respect, we gave Group E 2½ gm. of mash in the endbox and allowed them to eat it all, which took 90 to 120 sec. Group C *Ss* were removed after 30 sec. as before.

Results

Figure 1 shows mean revolutions per minute (rpm) for Groups E and C on successive test days. Breaks in the lines indicate the procedural changes noted above. The two sets of points may be seen to follow each other closely. "Student's" *t*, whether based on all days or only on days 11–19, fell far below the .05 level for 5 *df*.

To check the effectiveness of the food reward by another measure, each *S*'s median daily exit time was recorded. Figure 2 presents the means of these medians for the two groups. In a two-tailed test of the null hypothesis the mean of the mean intrapair differences for all days, 13.8 sec., gave a *t* of 3.07, significant at the .05 level.

Discussion

Two facts are clear: (*a*) Our results failed to confirm the effect of a food incentive on wheel-turning reported by Geier. (*b*) This failure could not be attributed to the absence of *any* incentive effect. Seeking another explanation, we thought of two possibilities:

1. When tested, Geier's rats were 4½ mo. old, ours less than 3½ mo. If our *Ss* were basically more active than his, the addition of

food tension might be unable to raise the activity level any higher. Geier reported a mean score of about 25 rpm for food trials, 14 rpm for nonfood trials. Corresponding means in our experiment were 29 and 28 rpm.

2. As already suggested, Geier's rewarded *S*s may have learned to turn the wheel through inadvertent food reinforcement. If this were the case it should be quite easy to induce a wheel-turning habit by judicious use of reward.

Experiment II was a test of the second hypothesis. Incidentally, it provided data, comparable with those of Experiment I, on older animals.

EXPERIMENT II

Method

Twelve male hooded rats were placed in activity cages at about 4½ mo. and lived in them throughout the experiment. After the first week they were fed for 1 hr. once a day in groups just after the time of experimenting.

Adaptation and matching trials. The same apparatus was used. Adaptation to it, which began on the third day, took a different form. These rats were originally selected with another purpose in mind, for which it was desirable to avoid any competition between turning the wheel and leaving it. The opaque exit door was therefore kept closed, permitting no access to alley or endbox. Since little wheel-turning appeared, a preliminary attempt was made to induce it by using light aversion. The room was darkened and two 60-w. lamps were mounted above the wheel. The *S* was put in with the lights on; when it ran, they were turned off for 15 sec. with the wheel stationary, then turned on for the next trial. Eight trials a day were given for five days, during which the number of revolutions required to darken the wheel was increased by steps from less than one to five. This level was maintained for the next four days with four trials a day. Two *S*s refused to run and were eliminated. No evidence of learning appeared in the time scores of these 16 trials. They were used, however, as a basis for matching the *S*s for the next part of the experiment.

TABLE 1

Confidence Levels for Rejecting the Hypothesis of No Improvement of Exit Times in Groups E and C

Subject	Group E	Group C
1	.002	.25
2	.09	.75
3	.09	.75
4	.09	.50
Composite	.001	.80

Test series. Since our rats were now 5 to 5½ mo. old, we decided to repeat Experiment I as a check on the influence of age. The wheel lights were no longer used. Subjects were assigned at random within matched pairs to Groups E and C and were given three spaced trials a day for six days. On each trial *S* was confined in the wheel for 1 min.; the exit door was then opened. Group E was permitted to eat the 2½ gm. of mash in the endbox; Group C found no food and was removed after 1 min.

Learning series. An attempt was now made to train the animals to turn the wheel for a food reward. Conditions remained the same except that the exit door was opened and the wheel braked as soon as *S* made three revolutions without stopping. *Wheel time,* defined as the time from putting the rat in the wheel until it made three continuous revolutions, was recorded by manual operation of an electric timer.

After six days incentive conditions were reversed. Group C now found 2½ gm. of mash in the endbox, while for Group E the dish was empty. Daily trials were increased from three to four and continued for six more days.

Results

Test series. One member of Group E failed to adjust to the experimental conditions; it and its control were eliminated from the data. Results for the other four pairs were essentially similar to those of Experiment I. Mean revolutions per minute for Group E was 19.3, for Group C, 23.7. Mean differences, E-C, within pairs were −10.8, −4.4, −2.4, and 0. The *t* for 3 *df* fell short of significance. Day-by-day scores revealed no trend in either group.

As in Experiment I, an incentive effect showed up in exit times. Here it took the form of improvement for Group E, none for Group C. Unfamiliarity of alley and endbox resulted in marked variability and missing scores. When a rat refused to leave the wheel within 1 min., it was urged gently into the alley. It was therefore impossible to compute means. Instead we stated a null hypothesis as follows: If *S* failed to improve, the true proportion of trials in the first half of the series with exit times below the median for the entire series would be at least 0.5 We then counted for each *S* the frequency of such trials in the first three days of the series. A table of the binomial distribution (15) enabled us to determine the probability of this frequency on the above hypothesis. Finally, we used the chi-square method described by Jones and Fiske (6) to determine the composite probability for each group. As shown in Table 1, the hypothesis can be rejected with confidence for Group E but not for Group C.

Learning series. One more member of Group E developed increasing resistance to eating in the apparatus and was dropped after the first six days. Eight *S*s, three in Group E and five in Group C, completed the series. Comparisons between matched *S*s were therefore not attempted. Use of a counterbalanced design also precluded pooling the groups to compare reinforced with nonreinforced trials, since interaction effects could neither be ruled out nor measured (7). Since our concern here was with improvement in wheel-turning as a function of reinforcement, we confined our treatment to the analysis of trends.

First we eliminated a few extreme values which met, at the .01 level, the test for gross errors given by Dixon and Massey (2, p. 243). Owing to the usual correlation between the means and variances of response times, we next transformed raw wheel times into logarithms. The mean log wheel time of each *S* on each day constituted the basic datum for analysis.

Figure 3 shows the daily means of these scores for each group with and without food reinforcement. Evidence of a downward trend with reinforcement appears in both groups. Analysis of variance showed the "days" effect in both curves to be significant at the .01 level.

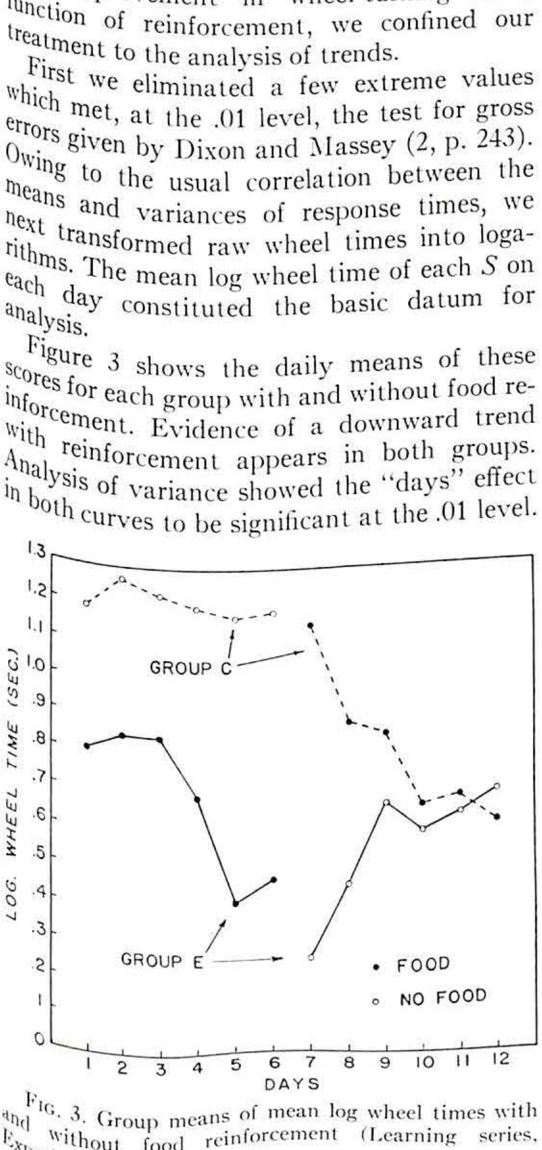

FIG. 3. Group means of mean log wheel times with and without food reinforcement (Learning series, Experiment II).

Comparing individual days in Group E we found significant differences ($p = .01$) between the first four and the last two days in all but one comparison. In Group C day 1 was similarly distinct from all subsequent days except the second. The opposite directions of curvature suggest a possible "latent learning" but should first be verified with larger samples.

Turning to the results without reinforcement, we find no trend in those of Group C. In Group E, however, the apparent rise after removal of food is confirmed by an F significant at the .05 level. Significant differences at the same level are found between the first day and all days later than the second.

DISCUSSION

Results of the test series gave no support to the hypothesis that the negative results of Experiment I were a function of the age of the animals. Although the reduction of sample size in Experiment II was regrettable, it is unlikely that adding more cases would alter this conclusion.

Results of the learning series were positive in one sense: they demonstrated that hungry rats will acquire increased readiness to turn a wheel if doing so leads directly to food. They also suggested that this increment may be subject to extinction. But in the sense that these results offer an explanation of Geier's finding, they, too, must be considered negative. Geier rewarded his experimental *S*s whether or not they turned the wheel. The learning we were able to induce by exclusively rewarding that response was neither so rapid nor so pronounced as to imply that it would occur through haphazard reinforcement.

Our attempt to exploit the activity wheel as a measure of goal striving resulted in a failure to confirm Geier's finding. Three interpretations are possible:

1. The concept of goal-induced drive is invalid.
2. The activity wheel cannot be used to measure that drive.
3. The activity wheel measures that drive only under special, at present unknown, conditions.

Against the first interpretation may be cited the recent study by Sheffield and Campbell (12). Using an activity cage of the stabilimeter type rather than a revolving drum, they obtained clear evidence of increased activity during a 5-min. environmental change on condition that it regularly preceded the daily feeding. This finding, together with the evidence cited by Maltzman (8) and Seward (11), strengthens the case for incentive motivation.

The second interpretation implies a source of error in Geier's study. Since there is no indication of what it might be, this conclusion should be adopted only as a last resort.

As to the third possibility, in Experiments I and II we have varied—not systematically, it is true—the following factors without effect: (*a*) delay of reward, (*b*) amount of reward, (*c*) distribution of trials, and (*d*) age of animals. Another factor remains to be examined: strength of drive. Consideration of this variable leads to the following hypothesis:

There is considerable evidence from early studies (see Munn [9]) that activity in the revolving drum is related to hunger. In the present experiment, therefore, with moderate hunger (Level 1) we may expect some wheel-turning in both experimental and control groups. In Group E we postulate in addition a general excitement aroused by fractional responses to food; with increased hunger this excitement reaches a point (Level 2) at which it produces more running in Group E than in Group C. As hunger is still further intensified, however, another effect supervenes: general excitement gives way to specifically goal-directed responses. At this point (Level 3) the difference between the two groups should disappear. Finally (Level 4) these food-oriented responses may compete so successfully with wheel-turning that Group E will actually fall below Group C. To reconcile the results at issue we need only assume that Geier's animals were tested at Level 2, while ours were at either Level 1 or 3. Although we have no independent measure of drive levels in the two studies, such a difference is quite conceivable.

Verification of the hypothesis calls for a full-scale investigation. Meanwhile two bits of related evidence may be cited:

1. Geier and Tolman (4) tested wheel-turning at different distances along a 24-ft. runway to food. They found that with decreasing distance revolutions per minute first increased, then diminished. Goal striving presumably varied inversely with distance, first facilitating, then inhibiting "restless activity." If goal-striving varies with drive strength, it should produce the same effect.

2. Birch (1) found medium degrees of hunger optimal for problem solving in chimpanzees. He interpreted his finding to mean that too little hunger failed to direct the *S*s' efforts toward the goal of food; too much hunger directed them toward it to the exclusion of the surrounding objects necessary to problem solution. Our reasoning with regard to wheel-turning is closely analogous.

SUMMARY

Experiment I was an attempt to confirm Geier's (3) finding that the amount of running by rats confined in an activity wheel for 1 min. was increased by feeding them immediately thereafter. Twelve rats matched for wheel-turning were assigned to experimental and control groups and tested under several conditions. No difference in revolutions per minute appeared between Groups E and C.

Experiment II, besides confirming Experiment I on older animals, showed that wheel-turning readiness could be increased by giving a food reward and decreased by removing it. This effect, however, was not striking enough to explain Geier's results.

A hypothesis was suggested to account for the discrepancy between the two studies.

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AN EXPERIMENTAL TEST OF AN ALLEGED INNATE SIGN STIMULUS

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The literature contains several reports (1, 2, 3, 4, 5) to the effect that a moving overhead "shape in relation to direction of movement" (5, p. 77) acts as a sign stimulus for domestic and other fowl independently of any previous experience with these configurations—i.e., the same shape in different directions serves as a sign to release different responses. Thus, Tinbergen (4, p. 35) reports that a cardboard model designed to look like a hawk (H) when flown in one direction "caused escape reactions, such as flight and crouching," whereas this same model when flown in the opposite direction looks like a goose (G) and elicits "merely superficial interest." None of these studies, however, reports the use of certain important controls such as the testing of individual birds and the use of birds with a known developmental history. We decided therefore to make such tests under controlled conditions on birds raised in the laboratory.

METHOD

Experimental Design

The stimulus variable of primary concern was "shape in relation to direction of movement" (5, p. 77). This variable was studied under eight conditions. Each of these conditions represented a cell in a trifactorial experiment designed to provide information about three variables that preliminary tests had indicated necessary to control. The first control variable, size of stimulus, was studied under two conditions: large (10-in. wing span), small (4-in. wing span). Order of presentation was investigated in two arrangements: HGHG, GHGH. The influence of shadow was also studied at two levels: presence of shadow, absence of shadow.

Subjects

The *S*s were 24 naive, eight-week-old, white Leghorn chickens. Twelve males and 12 females were distributed fairly evenly among the various conditions. The birds were obtained immediately after hatching from the incubator at the Poultry Husbandry Laboratory of the University of California. They were raised in a 5- by 5-ft. enclosure that included a brooding hut. This apparatus was kept in a different laboratory room from the one in which the experiment was performed. They were tended by one of the authors and all experience with flying objects was precluded.

Apparatus

The apparatus consisted of a straight alley 60 by 11 in. with wire sides 24 in. high. To facilitate observation, the alley was marked off into six sections each 10 in. long. The alley was open at the top except for one end-section, which was covered to serve as a potential shelter. The runway was situated on the floor inside a triangular enclosure, the sides of which—black Halloween cloth—served as a one-way observation screen.

The stimulus—a black cardboard model—"was made with symmetrical anterior and posterior wing edges. At one end of the body axis there was a short protuberance, at the other end a long one" (5. p. 77). "When pulled to the right, the model had a short neck and a long tail (hawk); when pulled to the left, it had a long neck and a short tail, ('goose')" (4, p. 35). The shape was copied from the picture shown in Tinbergen (4, p. 34) and also in Miller (3, p. 445). The stimulus was pulled over the length of the alley on a string track at a height of 105 in. It remained exposed from 1½ to 2 sec.

Procedure

The experiment lasted 4 min. beginning from the time that *S* was placed in the third section of the alley facing away from the shelter. For half the *S*s, at the end of the first 60 sec. the model was pulled to the right to appear like a hawk (short neck and long tail); at the end of the next 60 sec. the model was pulled back in the opposite direction to appear like a goose (long neck and short tail). The next two 60-sec. periods repeated the same sequence. Thus, for half the *S*s the order of presentation was HGHG. For the other half of the *S*s the stimulus was exposed in the reverse order, GHGH; thus, any effects that may have been due to order of presentation were counterbalanced. This condition is referred to as "order" in the analysis.

Nonsystematic preliminary tests on another group of animals had led us to believe that when no shadow was cast, a stimulus with a 4-in. wing span was below threshold. In the experiment proper the 4-in. size was therefore exposed to half the animals in order to control for noise and other extraneous influences, and also to test this finding systematically. A stimulus with a 10-in. wing span was exposed to the other half of the group. This condition is referred to as "size."

During the entire experimental period the room was illuminated by two 100-w. bulbs covered with milk-glass globes and suspended from the ceiling at a height of 115 in. In addition, there was a 60-w. light suspended at the same height directly over the center of the alley. During the testing of half the *S*s this lamp was lit so that a shadow was cast by the stimulus

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[1] The authors are indebted to Dr. Leo Postman for many helpful suggestions and criticisms.

TABLE 1

Analysis of Variance of Total Scores for Three Control Factors in Discrimination Test

Source of Variation	*df*	Mean Square	*F*	*p*
Order	1	1.5050		
Presence or absence of shadow	1	26.7337	8.514	$< .01$
Size	1	.9243		
Residual	20	3.1399		

TABLE 2

Analysis of Variance of Trial 1 Activity Scores in Discrimination Test

Source of Variation	*df*	Mean Square
Form (H vs. G)	1	.0187
*S*s within groups	23	.2192

TABLE 3

Analysis of Variance of Weighted Total Scores in Discrimination Test

Source of Variation	*df*	Mean Square
Order	1	.0051
*S*s within groups	23	.7218

passing under it. During the testing of the other half of the *S*s the center light was turned off so that no shadow was cast. This condition is referred to as "presence or absence of shadow."

The six response measures used were: (*a*) amount of activity as measured by the number of sections of alley traversed in a 5-sec. interval, (*b*) a group of qualitative responses—(1) darting forward, (2) walking, (3) crouching, (4) wing-flapping, (5) taking shelter. The selection of these responses as indicators of fear was based on our own preliminary observations and the discussion by Krätzig (1).

During the experiment proper, there were four persons in the room but outside the enclosure. Only one bird at a time was in the experimental room during the test session. Every 5 sec. two of the observers made independent ratings of the five fear responses while the third recorded the amount of activity. The fourth stepped inside the enclosure to place each bird in the alley at the start of a test period and to remove it at the end.

RESULTS

A separate analysis was performed on the measures obtained for each of the six types of response. The results of a typical one of these analyses are presented below.

The response in this analysis was amount of activity as measured by the number of sections of alley traversed per 5-sec. interval for the 15 sec. immediately following the exposure of the stimulus. Table 1 summarizes the analysis of variance performed on the three control variables—size of stimulus, order of presentation, and influence of shadow. The scores used in this analysis were the total number of responses (amount of activity) on the four trials for each *S*. Only the main effect due to the presence or absence of a shadow proved to be a statistically significant source of variation. Similar results were found in the other analyses.

Two further statistical tests were made to evaluate the stimulus variable of primary interest—shape in relation to direction of movement. First, the responses of the 12 *S*s that received the "hawk" image on trial 1 were compared with the responses of the 12 *S*s that received the "goose" image on trial 1 by means of a simple analysis of variance. The results of this analysis are summarized in Table 2. It is clear that no differential response to these two images was observed on the first trial since the mean square between conditions is smaller than the mean square within conditions. Next, weights were assigned to the individual trial scores in order to cancel out the over-all effects of trend in a counterbalanced design. The scores on trials 2 and 4 were assigned negative values (multiplied by -1), while the scores on trials 1 and 3 were left unchanged (multiplied by $+1$). A simple analysis of variance was then performed in which the scores consisted of the algebraic sum of these weighted response scores for the four trials for each *S*.[2] A summary of these results is presented in Table 3. Again, the mean square between groups is smaller than the mean square within groups, indicating that there was no differential reaction to these two stimulus configurations throughout the experiment.

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[2] If we let $i = 1, 2, 3, 4$ represent the particular trial observed, then an *S*'s score in this analysis is represented by $X_i = X_1 - X_2 + X_3 - X_4$. For this suggestion we are indebted to Professor Evelyn Fix of the Mathematical Statistics Laboratory, University of California.

Similar results were obtained from the analyses of the other response measures.

The analyses do not show the size effect to be a statistically significant source of variation. This result is not congruent with our earlier impression that the threshold is above 4 in. There is, however, a consistently greater response to the larger stimulus.

DISCUSSION

In general, we must conclude that under our conditions the hypothesis that certain specifically shaped sign stimuli innately arouse fear must be rejected in the case of the white Leghorn chicken. Evidence from the preliminary tests on another group of animals not included in this report casts further doubt on that hypothesis. For in the preliminary test we also used circles of various sizes as stimuli and obtained the same fear response provided the diameter exceeded 4 in. Tinbergen (5, p. 32) reported that a circle does not release an escape response. Whether or not the difference in results may be due to differences in setting—the laboratory versus the barnyard—is a question that our results cannot answer.

The preliminary tests also indicated the optimal stimulus exposure time to be the 1½- to 2-sec. interval used in the experiment proper. At that time the fear response was found to extinguish in 10 to 12 trials and to show spontaneous recovery after the passage of 2 to 3 hr.

Our observations in the laboratory lead us to conclude that four variables are important for eliciting the escape response in the chicken: amount of previous experience, rate of movement, size, and presence or absence of a shadow.

SUMMARY

The Tinbergen hypothesis that certain specifically shaped sign stimuli innately arouse a fear response was tested on the white Leghorn chicken and found to be untenable under controlled laboratory conditions.

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SHOCK INTENSITY AND AVOIDANCE LEARNING

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The parametric investigation of the influence of motivation on learning has largely been limited to the appetitive drives. Studies of the effectiveness of different levels of aversive motivation are surprisingly rare. In view of the recent increased interest in behavior based on fear, such studies become a matter of some interest. This is particularly true of shock, which is almost always used as the fear-producing stimulus in animal experiments when fear or anxiety is manipulated.

EXPERIMENT I

The literature on avoidance training contains a variety of descriptions of the allegedly typical behavior of rats in the presence of electric shock. Some authors (e.g., 3) stress the point that shock increases activity; others (e.g., 4) have claimed that inactivity is dominant in the hierarchy of reactions to shock. Two possibilities to account for such diversity of opinion suggest themselves. One is that rats are bimodally distributed in their reactions to shock, some being crouchers, others jumpers. The other is that shock intensity is the important variable and that different investigators have arrived at these different descriptions on the basis of results obtained under quite different shock levels. The purpose of experiment I was to obtain direct evidence on such matters. The method was a variation on the psychophysical method of limits in which the stimulus dimension was shock intensity.

Method

Apparatus. The apparatus was a box 9 in. high by 11 in. long by 4.5 in. wide, with an electrifiable grid as a floor and a clear Plexiglas front through which *S*'s behavior could be observed. An unavoidable shock of approximately 230 v. and controllable amperage was applied to the grid by a model 228 electronic stimulator manufactured by the C. J. Applegate Co. Shock duration was controlled by a Hunter-Brown electronic interval timer.

Subjects. The *Ss* in the experiment were 10 male albino rats of the Wistar strain, about 200 days old at the time of the experiment. They were housed in the animal colony and allowed free access to food and water.

Procedure. The *S* was placed in the apparatus for a 5-to 10-min. adaptation period, following which *E* administered 16 series of shocks according to a modified method-of-limits procedure. Each series consisted of ten stimulations ranging from 0.0 ma. to 0.9 ma. in 0.1-ma. steps. The series was presented in an ascending and descending order on alternate trials, with the first trial for each *S* always being an ascending series. The 0.0-ma. value served as a test for conditioned responses to slight noises coming from the apparatus. No *S* ever responded to them.

Each shock was of 1.0-sec. duration and shocks were spaced at 30-sec. intervals. The intensity range, duration, and spacing of shocks were based on experience with perhaps a dozen preliminary animals. Experience with the preliminary *Ss* also gave *E* practice in noting and recording their responses.

Response measures. The *E* noted *S*'s response to each shock and recorded it in one of three categories determined by preliminary observations: (*a*) no response, (*b*) jump, and (*c*) flinch. This last response category requires comment. We defined this response as a startle response to shock in which *S*'s feet did not leave the grid. We suspect that this flinch response is what other investigators (4, 5) have called a "crouch" or "freeze"; but without having observed the behavior of other *Ss*, we cannot be sure. The data were collected by two different *Es* who began the experiment only after they had run enough practice *Ss* to reach a high degree of agreement on the response categories.

Results

As a function of shock intensity the jump and flinch responses were different. The graph in Figure 1 shows the mean percentage of jump and flinch responses at each shock intensity, omitting the points for the 0.0-ma. intensity to which no *S* responded. The frequency of jump responses increases steadily with shock intensity, whereas the frequency of flinch responses decreases beyond 0.3 ma. Clearly the flinch response is one to low intensities of shock. Every *S* produced some such responses but no *S* gave them predominantly. If it is assumed that the flinch response is the same as the crouch response noted by other authors, it is obvious that rats are distributed bimodally in response to shock only at rather low intensities (0.2 to 0.5 ma.). At higher shock levels, at least for the strain of rats sampled here, all

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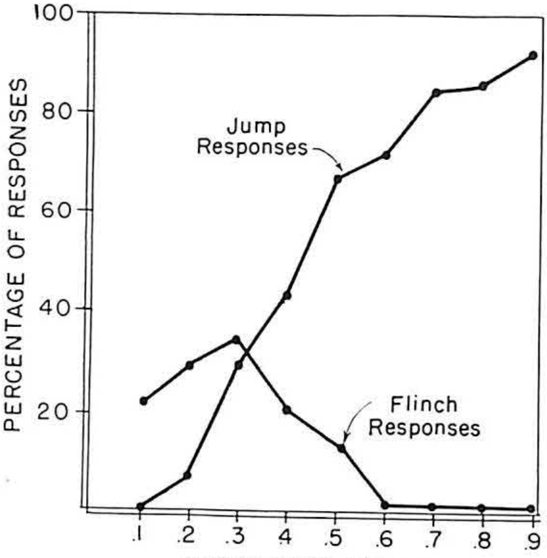

FIG. 1. Percentage of jump and flinch responses as a function of shock intensity.

rats are jumpers. A comparison of shock thresholds in the first and second halves of the experiment shows that there was some adaptation. The mean shock intensity at which a jump response occurred 50 per cent of the time was 0.36 ma. during the first eight series of shocks and 0.51 ma. during the second eight series of shocks. Although this change in sensitivity is statistically reliable ($t = 4.05$, $p < .005$), the chief significance of the finding seems to us to lie in the fact that, in almost 150 closely spaced trials, the threshold increased only 0.15 ma.

EXPERIMENT II

This experiment compared the acquisition and extinction of a wheel-turning habit where the shock used as the UCS was 0.2 ma., 0.5 ma., 1.0 ma., or 2.0 ma. The results of the previous experiment indicate that this range of shocks extends from a relatively weak one to a very strong one. The results of this experiment, therefore, should produce a good first approximation to the function relating performance in this situation to the intensity of the UCS. From the previous experiment, we also know something about the kind of UCR's which these various shock levels will evoke from the *S*s. For the weakest shock, they will be predominantly flinch responses; stronger shocks will produce fewer of these, and more jump responses. This raises two important points: (*a*) The precise pattern of behavior developed in the *S*s conditioned under the various UCS intensities will probably be different. (*b*) On the reasonable assumption that the jump response is more nearly compatible with wheel-turning than the flinch response, any reduction in performance under weak shock intensities may very well be attributed to the occurrence of incompatible flinch responses. Finally, from the earlier experiment we know that performance will not be complicated much by adaptation if the number of shock trials is less than 50 or so.

Method

Apparatus. The apparatus used in this experiment was a wheel-turning one, consisting of a box 6 in. high, 4.5 in. wide, and 9 in. long, with a movable wheel inserted in one end. The floor was an electrifiable grid and the front wall was of transparent Plexiglas. Timing and shock level were controlled by the same equipment as was used in the preliminary experiment.

The CS was a muffled buzzer which came on 5 sec. before the shock and continued until *S* responded. If *S* turned the wheel in the 5-sec. interstimulus interval, the shock did not come on and the CS went off immediately. If *S* responded after the onset of shock, the CS and UCS went off together.

In an effort to eliminate what have seemed, in previous experiments with apparatus similar to this (1), an unduly larger number of responses to extraneous stimuli and to the animals' own fear, this apparatus was wired so that the CS could be presented only after a period in which *S* did not turn the wheel. Specifically, starting a trial initiated a 3-sec. "dead period" terminated by the presentation of the CS. If *S* turned the wheel during this period, the CS and UCS did not come on, and *E* had to start the trial again.

Subjects. The *S*s were 91 male albino rats, 150 to 200 days old, of the Wistar strain. They were housed in the animal colony and allowed free access to food and water. Seven of these rats constituted a control group that received trials on which the buzzer sounded but the shock did not come on. Because of their failure to provide any data, no additional *S*s were used in this condition. The other *S*s were conditioned at 0.2 ma., 0.5 ma., 1.0 ma., and 2.0 ma. in groups of 21.

Procedure. Many of the procedural details followed those of the first experiment. The *S* was placed in the apparatus for a 5- to 10-min. adaptation period. Then *E* administered 30 conditioning trials at a minimum intertrial interval of 30 sec. The early trials were separated by more than this because of spontaneous wheel-turning. If *S* did not respond in 15 sec., *E* terminated the trial and started a new one 30 sec. later. Following the training trials, *S* was extinguished to a criterion of four successive trials on which a response did not occur within 15 sec. As in training, the intertrial interval was 30 sec.

The assignment of *S*s to experimental conditions was done at random for the 0.2 ma., 0.5 ma., 1.0 ma. and 2.0 ma. groups for squads of four *S*s. The experimental design, thus, was a treatments replications factorial, with a single *S* occupying each cell. The error term in such a design is the interaction variance. Although this design sacrificed 20 *df* in the present experiment, it was used as the most efficient one available. Previous experience with avoidance learning data led us to anticipate positive skewing on both response measures, latency and resistance to extinction. Ordinary analysis of variance is inapplicable to such data. The interaction terms upon which the error estimate is based in the factorial experiment, however, tend to be more nearly normal in their distribution, even when the scores within groups are skewed (2, p. 161).

Results and Discussion

The function relating performance to shock intensity during training appears in Figure 2 in terms of average response latency on the last 15 trials. The measures in Figure 2 were derived in the following way. First learning curves were constructed based on median latencies for trials in blocks of five. These curves appeared to be asymptotic, or nearly so, during the last three blocks of trials. On this ground, the median latencies for these blocks of trials were averaged for each *S*, and the mean of these averaged median latencies was plotted in Figure 2. The value plotted for the 0.0 ma. group is obviously underestimated because of our procedure of stopping a trial after 15 sec. (criterion latency) without a response. Statistically the differences indicated in Figure 2 are reliable. An analysis of variance which excluded the 0.0 ma. group produced an *F* ratio of 15.05, which, for 3 and 60 *df*, is significant at the .001 level. Extinction measures for the same four groups on the other hand, were highly variable and not significantly different. Analyses of variance on the number of trials to the extinction criterion and on the number of extinction responses with latencies of 5.0 sec. or less produced, in each case, an error variance larger than that for the effect of shock intensity. Such a failure for extinction measures to reflect differences obtained during the training presents a problem. The usual assumption is that avoidance responses are mediated by a learned fear. On this assumption, the better performance of the *S*s trained under very strong shock can be explained in terms of a greater fear. But, on the same assumption, one would suppose that the greater fear would persist into the extinction period and that resistance to extinction would be greater after conditioning with a strong shock. The usual theorizing about avoidance learning thus encounters difficulty in treating these extinction data. It may be that studying the extinction of avoidance responses will provide a means of arriving at a more exact statement of the role of fear in the mediation of behavior.

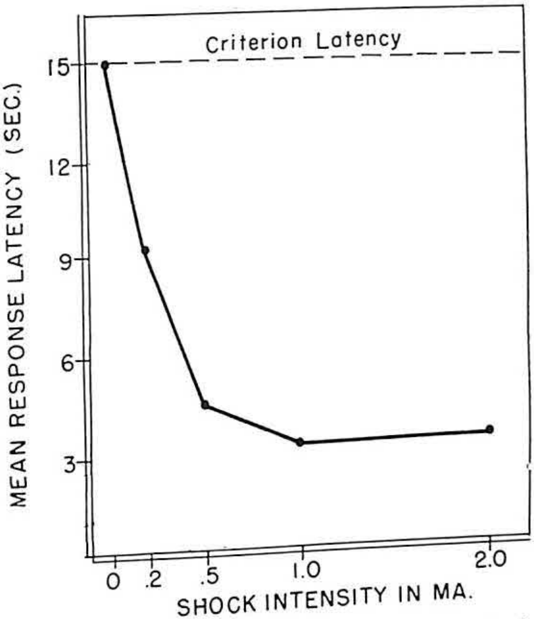

FIG. 2. Response latency as a function of shock intensity.

SUMMARY

The two experiments reported in this paper investigated the responses of the white rat to electric shock of different intensities. The first experiment employed a psychophysical method-of-limits procedure in which *E* observed presumably innate responses of ten rats to shocks in the range from 0.0 ma. to 0.9 ma. Results in terms of "jump" and "flinch" responses show that the former increases steadily with increasing shock intensity. The latter increases up to about 0.3 ma. and then decreases. Statistically dependable ($p < .005$) evidence for adaptation to the shock was obtained by comparing mean shock thresholds in the first and second halves of the experiment.

In the second experiment, four groups of 21 rats each were conditioned and extinguished in a wheel-turning, avoidance-training apparatus with a buzzer as the CS and a shock as the UCS. The shock intensities employed were 0.2 ma., 0.5 ma., 1.0 ma., and 2.0 ma. An additional control group of seven rats received a series of trials without shock, but these *S*s showed no evidence of learning. It was found that, during training, response latency decreased as a negatively accelerated function of shock intensity. During extinction, however, no statistically significant residual effects remained.

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TRAUMATIC AVOIDANCE LEARNING: THE EFFECTS OF CS-US INTERVAL WITH A DELAYED-CONDITIONING PROCEDURE

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Though the phenomenon of avoidance learning poses definite problems for theories of learning, serious attention to obvious parameters has been lacking. In particular, the effects of varying the time interval between the conditioned stimulus (signal) and unconditioned stimulus (noxious, prepotent stimulus) have been, until quite recently, unknown. True, an early study by Warner (11) showed that rats require more trials to reach an avoidance criterion as the CS-US interval is increased. But Warner's rats had been pretrained to escape from shock before they were introduced to the danger signal, and so are not comparable with *S*s in the usual avoidance training procedure. Then, too, Warner presented no analysis of extinction, and several theoretically important quantitative aspects of acquisition were not discussed.

Kamin's recent experiment (1) represents the first detailed analysis of the effects of CS-US interval on characteristics of acquisition and extinction of learned avoidance responses. Kamin used an intense traumatic shock as US. He used four CS-US intervals: 5, 10, 20, and 40 sec. What is most important for our experiment is the fact that Kamin used a CS of 2-sec. fixed duration, and so the CS always terminated *before* the onset of the US. Of course, this is the Pavlovian *trace*-conditioning procedure. In contrast, the Pavlovian *delayed*-conditioning procedure maintains the presentation of the CS until the US is presented and often maintains it until the US is terminated. In an avoidance learning experiment this would require that the CS remain during the entire CS-US interval and terminate when the US is terminated. The present experiment was undertaken to contrast and compare the effects of CS-US interval in Kamin's trace-conditioning procedure with the effects of CS-US interval in a delayed-conditioning procedure. Furthermore, it seemed possible that data bearing on these interesting questions might be obtained: (*a*) Is there good evidence of Pavlovian *inhibition of delay* in traumatic avoidance learning? (*b*) Since the delayed-conditioning procedure allows the CS to "bridge the gap" between CS onset and US onset, does it yield quicker acquisition of avoidance than does the trace-conditioning procedure, for identical CS-US intervals? (*c*) Since in the delayed-conditioning procedure the CS is terminated by the instrumental avoidance response, does it produce higher resistance to extinction than in the trace-conditioning procedure where the CS terminates arbitrarily? (*d*) Does CS termination in the delayed-conditioning procedure enter as a strong condition of reinforcement and thus tend to mitigate the effects of increasing the CS-US interval which were demonstrated by Kamin?

METHOD

Subjects

The *S*s were 85 mongrel dogs, maintained on an ad libitum food and water schedule, and in apparent good health during the experiment.

Apparatus

The apparatus was the same modification of the Mowrer-Miller shuttlebox used previously by Solomon and Wynne (9), Solomon, Kamin, and Wynne (8), and Kamin (1). It consisted of two identically built compartments separated by a barrier which was adjustable in height. A drop-gate hung above the barrier and could be lowered to rest upon it, thus separating the two compartments completely. Above each compartment hung two 40-w. lights. The voltage applied to the grid floor of the compartments varied slightly from dog to dog, since the traumatizing procedure, standardized in previous experiments, required that the highest subtetanizing current possible be used. This current was about 8 to 10 ma. for most *S*s, and served as the US. The CS was composed of the raising of the drop-gate and the simultaneous turning off of the lights directly above the compartment occupied by *S*. A more complete description of the apparatus and standard procedures is available elsewhere (8, 9).

Design

The experimental design provided for a direct test of the effects of the CS-US parameter. There were six

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[1] This research was supported by a grant from the Rockefeller Foundation and was facilitated by the Laboratory of Social Relations, Harvard University.

experimental groups, each treated identically except for the magnitude of the CS-US interval. The CS-US interval was held constant for a given *S*, but different groups were trained with intervals of 2.5, 5, 10, 20, 40, and 80 sec., respectively. There were 30 *S*s in the 10-sec. group; all other groups contained 11 *S*s each.

Procedure

The barrier between the two compartments was set at the height of *S*'s back, and *S* was placed in one compartment with the drop-gate down (closed). After a 10-min. acclimation period, ten pretest trials were conducted, on each of which the CS alone was presented. The compound CS plunged *S* into relative darkness in its own compartment and at the same time revealed the opposite compartment. If, after a 2-min. interval *S* had not jumped over the barrier into the other compartment, the drop-gate was lowered and the lights were turned on. The next pretest trial was started after a 1-min. interval, and so the time interval between CS presentations (trials) was 3 min. Ten pretest trials were given, to discover "jumpers" (*S*s whose operant level for jumping over the barrier was greater than zero); persistent jumpers were not used in the experiment.

Acquisition. On the day following the pretest, traumatic avoidance training was begun. After the usual 10-min. acclimation period in one compartment, the compound CS was presented; and after the appropriate CS-US interval, the traumatic US (subtetanizing shock) was turned on. The CS and US remained on until *S* escaped from the electrified compartment by jumping into the opposite compartment, which was, at that moment, lighted and unelectrified. After the escape, the drop-gate was quickly lowered to prevent retracing. Thus, both CS and US were terminated by the escape response (jumping). The next trial was started 3 min. after the last presentation of the CS; there were ten trials each day. The procedure required *S* to jump back and forth between the two compartments, with the direction of the jump reversed on alternate trials. Thus, there was no safe place in the long run; there was only a particular response which terminated the shock during the first few training trials. If *S* jumped at any time with a response latency shorter than the duration of the CS-US interval, the CS was terminated and the shock was omitted; this was an avoidance response, as contrasted with escape repsonses on trials where the response latency was longer than the CS-US interval. Response latencies were recorded by stop watch to the nearest .1 sec. The criterion of successful avoidance learning was ten avoidances in ten successive trials on one day. After meeting this criterion, *S* was never shocked to induce jumping, even if its latencies lengthened beyond the magnitude of the CS-US interval used in its training.

TABLE 1

Indices of Acquisition as a Function of the Length of CS-US Interval

Index		CS-US Interval (seconds)					
		2.5	5	10	20	40	80
Trial number of first avoidance	M	5.4	5.6	5.5	6.0	8.8	4.3
	Mdn	6	6	5	5	8	4
Trial number of last shock	M	15.7	10.8	12.3	12.3	14.3	16.5
	Mdn	12	9	12	12	12	16
Number of shocks received	M	7.6	7.2	7.8	9.1	11.5	10.2
	Mdn	6	6	7	9	10	8

Extinction. The extinction procedures described in detail by Solomon, Kamin, and Wynne (8) were used. All 85 dogs, after they had met the acquisition criterion, were randomly assigned to one of two main extinction groups: the *long*, regular extinction group or the *short*, regular extinction group. The *S*s in the short group received only one day (10 trials) of regular extinction after meeting the 10/10 criterion, while *S*s in the long group received 20 days (200 trials) of regular extinction. The regular extinction procedure merely presented *S* with the CS and did not allow *S* to be shocked for not quickly jumping, i.e., shock reinforcement was omitted. If an *S* in the short group did not stop jumping after its one day of regular extinction, it was subjected to special procedures designed to facilitate extinction; in the long group, special procedures were instituted if *S* failed to extinguish after 20 days of the regular extinction procedure. The special procedures were: (*a*) *shock extinction*—*S* jumped into shock if it jumped at all, and (*b*) *glass-barrier extinction*—*S* was prevented from jumping on some trials by the presence of a plate of glass between the two compartments. If, after regular extinction plus 100 trials of a special procedure, *S* had not stopped jumping, a combination of the shock extinction and glass-barrier extinction procedures was used; *S* was shocked for jumping when the glass barrier was absent, and on some trials *S* was prevented from jumping to the CS by the presence of the glass barrier. If, after 100 trials of this combined special procedure, *S* had not extinguished, *S* was declared a "failure to extinguish" case and was terminated. A criterion of "no jumping response" on ten successive presentations of the CS on one day was used to define the attainment of extinction. "No jump" was arbitrarily defined as a latency of 2 min.

RESULTS

Acquisition

The number of training trials required to achieve the first avoidance response. The first avoidance response is theoretically important because it is the first jump made by *S* in the presence of the CS without the motivating presence of the US. In Table 1 are listed the mean and median of training trials required to produce the first avoidance response for all CS-US interval groups. It is clear that the 80-sec. group represents a sharp reversal of a trend in which the learning index increases as the CS-US interval increases. There is a significant nonlinear regression ($p = .01$)

from 2.5 to 80 sec., but a negligible linear regression. The effect of CS-US interval on the emergence of the first avoidance response is, therefore, slight but detectable.

The number of training trials required to reach the last shock (escape) trial. The last shock trial is the last escape response before *S* embarks on its ten criterion trials. It is thus the trial on which the sequential variation between escape and avoidance responses terminates. It is an index of the difficulty *S* has in attaining invariant avoidance. The mean and median number of trials required to attain the last shock trial are listed in Table 1 for all CS-US interval groups. There is a significant linear trend ($p = .05$) for the index to increase from 5 sec. to 80 sec. The 2.5-sec. group gives a sharp reversal of the trend, probably because this group is being pushed to its physiological limit in maintaining consistent, short response latencies.

The number of shocks required before S attains the avoidance criterion. Since there normally is a wide variety of sequential variations of escape and avoidance responses during training, the number of trials required to reach the last shock trial is not equivalent to the number of shocks *S* receives during training. The number-of-shocks index may be thought of as the frequency with which *primary* reinforcement is required in the establishment of consistent avoidance responses. The mean and median numbers of shocks required for learning are listed in Table 1 for all CS-US intervals. There is a general tendency for *S* to require more shocks at the longer CS-US intervals. Both linear and nonlinear regressions are significant (linear: $.05 > p > .01$; nonlinear: $p < .01$), indicating that the two extreme groups (2.5 sec. and 80 sec.) are departing from a linear trend. It is clear, however, that the absolute magnitude of the trend is not very great, though certainly detectable.

Latencies of escape responses. There were no detectable differences between mean escape response latencies across the six CS-US groups. In all groups the escape latencies decreased rapidly to a point where *S* rarely remained in the presence of shock for more than 5.0 sec. before jumping. For the last three escape responses before meeting the acquisition criterion, the median escape latencies varied only from 1.8 sec. to 3.5 sec. across groups, and there was no detectable trend from short to long CS-US intervals. The median escape latencies on the trial preceding the first avoidance response ranged from 2.5 sec. to 4.8 sec., with no consistent trend across CS-US intervals. These are shown in Table 2.

TABLE 2

Latencies of Jumping Responses in Seconds at Various Stages in Avoidance Learning, as a Function of CS-US Interval

Latencies		CS-US Interval (seconds)					
		2.5	5	10	20	40	80
On trial before first avoidance	M Mdn	7.5 4.8	13.8 3.8	8.4 2.6	7.3 2.5	7.4 3.2	10.5 3.8
On first avoidance trial	M Mdn	2.3 2.4	3.5 3.4	6.2 5.1	4.8 2.8	12.4 10.8	11.2 9.2
On first ten trials after last shock	M Mdn	1.7 1.6	2.4 2.1	3.2 2.5	4.2 2.8	5.4 3.8	6.5 3.8
On twentieth day of regular extinction*	M Mdn	2.2 1.7		1.8 1.6	1.9 1.8	3.8 3.0	8.0 3.6
Difference between last shock trial and first criterion trial	M Mdn	−0.5 −0.2	+1.1 +0.7	+0.5 +0.9	+1.0 +0.7	+5.9 +5.5	+12.1 +6.7

* Not enough dogs in the 5-sec. group were carried through 200 extinction trials to warrant measures of central tendency.

Latencies of the first avoidance response. This measure may be taken as an index of the effectiveness of the CS in arousing a jumping response without the action of the US and in the absence of any prior avoidance experience. The mean and median response latencies for the first avoidance response are listed in Table 2, as a function of CS-US interval. There is a clear trend; the latencies of response are shorter for the shorter CS-US interval groups (p for both linear and nonlinear trend is .01). (See Fig. 1.) The latency of the first avoidance response, though taking place without the impetus of coexistent shock, reflects the conditions under which CS and US were paired on prior training trials.

Latencies of avoidances on the criterion trials. The mean and median avoidance response latencies for all ten criterion trials are listed in Table 2. The values are clearly an orderly

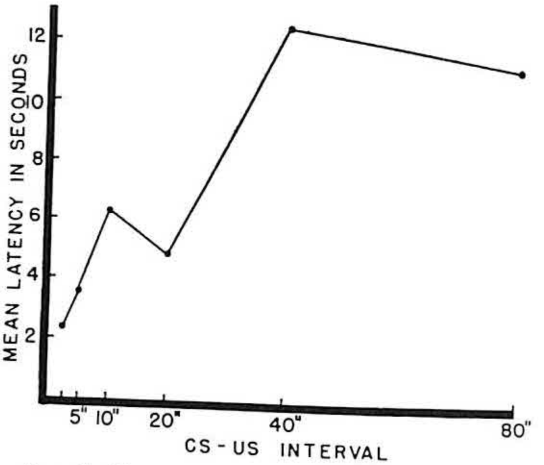

FIG. 1. The mean latency of the first avoidance response as a function of the CS-US interval used in avoidance training.

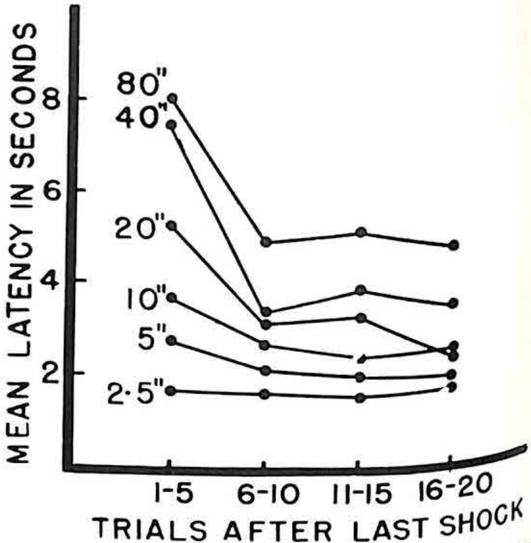

FIG. 2. The mean latency of avoidance responses on the first 20 trials following the last shock trial. CS-US interval used in training is the parameter. Each point represents the mean of five trials.

function of the CS-US interval; in general, the achievement of the avoidance learning criterion is accomplished with responses of longer latency for the longer CS-US interval groups (p for both linear and nonlinear trend is .01).

The absolute difference in response latency between the last shock trial and the first criterion avoidance trial. On the last escape (shock) trial *S* responds only after the US has been presented, and the escape response latency is the time that elapses between US onset and the jumping response. On the very next trial, *S* embarks on its criterion avoidances, and its response latency on such trials is the time elapsing between CS onset and the jumping response. The absolute differences between the response latency characteristics of these two adjacent trials reveal the extent to which the response to the US is of the same order of magnitude as the response to the CS alone. These differences are listed in Table 2 as a function of CS-US interval. The values clearly indicate that the latency characteristics of the first criterion avoidance trial cannot be perfectly predicted by the escape response latencies of the last shock trial. In general, the longer the CS-US interval, the greater the discrepancy between the two latencies. However, it is clear that the avoidance response latencies are much more accurately predicted by a knowledge of the escape latency on the last shock trial than by the magnitude of the CS-US interval used in training. For example, with a 20-sec. CS-US interval, the mean escape latency of the last shock trial was 4.4 sec., and the mean avoidance latency of the first criterion avoidance was 5.4 sec.

Extinction

Latencies during regular extinction procedure. In Figure 2 are plotted the mean latencies of the first 20 trials following the last shock trial, with CS-US interval as parameter. There are two clear results: (*a*) Despite the fact that no shocks are being received by *S*, latencies continue to shorten in an orderly manner. This confirms the findings of Solomon, Kamin, and Wynne (8). (*b*) The apparent avoidance latency asymptote is clearly a function of the CS-US parameter. This generalization holds for both the long extinction and short extinction groups; however, in the long extinction group the differences between the response latencies of the CS-US groups are small after 200 regular extinction trials, and it is only the 40-sec. and 80-sec. groups that clearly show the effects of the differential training conditions. There were no signs of impending cessation of responding in either the short or long extinction groups.

Behavior during the shock extinction period. After the dogs failed to extinguish during short and long regular extinction procedures, some were subjected to shock *for* jumping—the shock extinction procedure. There were no reliable differences among the CS-US groups in resistance to shock extinction. Nevertheless, there is some tendency for the *S*s in the 2.5-sec. and 80-sec. groups to be more prone to extinction. In general, shock extinction was not very successful in eliminating the jumping response. Only 57 per cent of all *S*s extinguished. The immediate effect of shocking animals for jumping was a *decrease* in response latencies. If *S* extinguished, it usually did so on the first day's trials; otherwise, *S* continued to jump into shock for 100 trials, with response latencies *shorter* than those observed during the regular extinction procedure! Thus, extinction brought about by a shock deterrent tended to be an all-or-none affair.

Behavior during the glass-barrier extinction procedure. Some *S*s were subjected to the glass-barrier, reality-testing extinction procedure after they had received their regular extinction trials. There were no orderly relationships between CS-US interval and behavior during glass-barrier extinction. Only 41 per cent of all *S*s extinguished during 100 trials of this procedure. The immediate effect of the glass-barrier procedure was a lengthening of response latencies across all CS-US groups. Animals not extinguishing showed *longer* latencies at the end of these extinction trials than they had during the regular extinction trials.

Behavior during the combined shock extinction and glass-barrier extinction procedure. Those *S*s that were still jumping after being subjected to either shock extinction or glass-barrier extinction were treated with a combination of the two; on some trials they were shocked for jumping, and on the others they were prevented from jumping by the glass barrier. There were no significant differences in resistance to extinction in the combined procedure across CS-US intervals. The *S*s that had the glass-barrier procedure prior to the combined procedure extinguished more easily in the four longest CS-US interval groups than did *S*s that had received the shock extinction treatment.

Emotionality

During acquisition. All *S*s in all groups showed conditioned emotional reactions to the CS on trials prior to the appearance of the first avoidance response. These emotional reactions included vocalization, defecation, urination, shivering, tensing, gasping, or inhibition of panting. There appeared to be more continued agitation in the long CS-US groups, during the intertrial waiting periods, than in the short CS-US groups. Vomiting and retching, when it occurred, was seen only in the 20-, 40-, and 80-sec. groups. Such qualitative observations must be interpreted with care, but they are similar to the observations made by Kamin (1).

During regular extinction. All *S*s gradually calmed down after learning to avoid the US. Vocalization, defecation, urination, trembling, and drooling tended to decrease in frequency and intensity, according to our recorded protocols. Panting tended to persist, even after 200 regular extinction trials, in all CS-US groups.

TABLE 3

Comparison Between Our Delayed-Conditioning Procedure and Kamin's Trace-Conditioning Procedure for Several Indices of Learning for Matched CS-US Intervals

(All values are means)

Index	CS-US Interval (seconds)							
	5		10		20		40	
	Delay	Trace	Delay	Trace	Delay	Trace	Delay	Trace
Trial of first avoidance response	5.6	4.5	5.5	5.1	6.0	6.9	8.8	17.0
Last shock trial	10.8	9.4	12.3	16.0	12.3	25.8	14.3	55.5
Number of shocks received	7.2	6.5	7.8	11.0	9.1	18.7	11.5	44.3
Latency of first avoidance (seconds)	3.5	3.0	6.2	4.3	4.8	9.2	12.4	10.7
Mean latency of five trials after last shock (seconds)	2.7	2.4	3.6	4.0	5.2	6.7	7.4	13.4

Resistance to being placed in the apparatus by *E* decreased markedly.

Comparison of Delay and Trace Procedures

The comparison of our results, derived from a delayed-conditioning procedure, with those of Kamin, derived from a trace-conditioning procedure, is not as straightforward as we might like. There were minor procedural differences which make the comparison only an approximation. In the first place, Kamin used an auditory CS; we used a compound visual and auditory CS. Secondly, Kamin allowed free responding and did not prevent retracing. Despite these differences, we strongly feel that the comparison is worth while, that the minor procedural differences will not invalidate our interpretation of the data to an appreciable extent.

Kamin used four CS-US intervals; we have matched our appropriate groups with his for 5, 10, 20, and 40 sec., respectively. In Table 3 are listed the more important indices of behavior during acquisition for our delay and his trace procedures. Two facts stand out. First, in *every* case the CS-US interval was a highly significant determinant of the magnitude of the index in *both* procedures. Secondly, some indices showed a significant *interaction* effect existing between the CS-US variable and the delay-trace distinction. This interaction effect was small for the mean trial number on which the first avoidance occurred; but it was highly significant for the mean trial number on which the last shock was received and for the mean number of shocks required to achieve the avoidance learning criterion. These significant interactions arose because the CS-US interval, as it increased in magnitude, caused a relatively greater hindrance to learning in the trace-conditioning procedure. In using the delayed-conditioning procedure, the effects of lengthening the CS-US interval were "flattened out" and mitigated.

In our experiment we obtained no cessation of jumping to the CS when we used the regular extinction procedure for 200 trials. This is in marked contrast to Kamin's findings, since he observed fairly rapid extinction of jumping for his 20- and 40-sec. groups. Half his 5-sec. group and 20 per cent of his 10-sec. group failed to extinguish in 100 trials. Kamin's 5- and 10-sec. dogs, during regular extinction procedures, showed decreasing latencies for a few trials after meeting his acquisition criterion, and then latencies began to increase. In the 20- and 40-sec. groups there was no shortening of latencies; instead, the lengthening of latencies was quite precipitous; but in the 5- and 10-sec. groups, the increase was gradual and slow.

DISCUSSION

The results of this experiment can be interpreted with some success in terms of a modified two-process theory of avoidance learning. This theory has been described in detail in previous papers (8, 9, 10). It is derived from the formulations of Miller (2), Mowrer (3), and Schlosberg (7).

We assume two processes in the acquisition of avoidance. One, Pavlovian conditioning, underlies the development of conditioned emotional reactions. The empirical laws of classical conditioning apply to this process, and so the three most important variables would be: (*a*) the magnitude of the CS-US interval, (*b*) the intensity of the US, and (*c*) the intensity or vividness of the CS. The development of the conditioned emotional reactions (in this case, anxiety reactions) depends upon the temporal pairing of CS *onset* and US *onset*. Drive reduction is assumed not to affect this process. The second process, in contrast, emphasizes drive reduction or relief, and it underlies the development of the learned instrumental jumping responses. The reinforcement of the jumping response is assumed to stem directly from US termination on escape trials and CS termination on avoidance trials. Here, the most important variables would be: (*a*) the time interval between the jumping response and CS or US termination, (*b*) the amount of reinforcement, or rate and magnitude of relief, and (*c*) the intensity or vividness of the CS. The two processes are thought to be independently manipulable, but during avoidance training they become highly related when the conditioned emotional reaction elicited by the CS becomes intense enough to produce an internal stimulus pattern having drive properties. Such response-produced drive stimuli can be terminated by the removal of the eliciting CS by appropriate instrumental acts.

According to this analysis, the first avoidance response occurs when the anxiety reaction elicited by the CS is intense enough to be similar to the original pain-fear reaction elicited by the US. The *S* is motivated to jump to the CS in the absence of shock. Solomon and Wynne (9), in their detailed analysis of acquisition of avoidance, postulated that the latency of the first avoidance response was a compounding of two latencies: (*a*) the latency of the anxiety reaction to the CS was thought to be about 2.5 sec.; and (*b*) the latency of the jumping response to a stimulus was thought to be about 2.0 sec., giving a total latency of about 4.5 sec. Conveniently enough, the median latency of the first avoidance response was 5.1 sec. for Solomon and Wynne's dogs, and this coincidence led them to predict that this latency value would be a constant, no matter what the CS-US interval might be and no matter how many trials it required to produce the first avoidance. Of course, the data from our experiment invalidate this prediction because first avoidance latencies lengthened with increasing CS-US intervals. Evidently, the conditioned emotional reaction to the CS is subject to some sort of inhibition-of-delay factor like that described by Pavlov. However, the inhibitory factor is not strong, or else we would have found first avoidance latencies to approach the magnitude of the CS-US interval. The effective intensity of the anxiety reaction must increase rapidly after the CS onset, achieving an intensity value of drive proportions long before the end of the CS-US interval. However, the number of trials required for the anxiety reaction to acquire this intensity is, in turn, a function of CS-US interval.

Our findings refute a signal-switching interpretation of avoidance acquisition. The median escape latencies on the trial just preceding the first avoidance response would predict a first avoidance latency of about 3 to 5 sec. for all CS-US groups if the jumping response were merely being switched from the control of the US to the control of the CS. Instead, first avoidance latencies were a function of CS-US interval, and were generally longer than 3 to 5 sec.

Our delayed-conditioning procedure produced approximately the same first avoidance latencies for each CS-US group as did Kamin's trace-conditioning procedure. This means that CS *duration* cannot be very important in determining the characteristics of the *first* avoidance response; rather, the time interval between *CS onset* and *US onset* must be the ruling factor.

At first glance, one might attribute any differences between the trace and delay procedures to the "bridging-the-gap" function of the persisting CS in the delayed-conditioning procedure. This, however, is probably not a good interpretation, because the mean trial of the first avoidance response and the first avoidance mean latency reveal no significant differences between the two training procedures. If the *persisting* CS in the delay procedure were serving to facilitate the establishment of some sort of "associative bond" between CS and US, we would expect the first avoidance response to appear earlier in training, and with shorter latency than it would in the trace procedure. This was not so. Therefore, the main effect of the *persisting* CS must be due to its conditions of *termination*. In the delay procedure CS termination is contiguous with the jumping response, and the reinforcing effect should be optimal. This interpretation agrees with the findings of Mowrer and Lamoreaux (5).

Once the first avoidance response has occurred, the action of reinforcement through *CS termination* and anxiety reduction should become very important in maintaining short latency responses. This means that CS duration should be a critical factor in determining how quickly the learning criterion is achieved. A comparison of the trace and delay procedures does not invalidate this assumption. The trace procedure required more shocks and more trials to reach criterion than did the delay procedure; and this difference increased as CS-US interval increased. In the trace procedure only the 5-sec. group had response latencies short enough to enable the jumping responses to receive the benefit of simultaneous CS termination, while *all* of the delay procedure groups received this benefit. Thus, the effect of lengthening the CS-US interval is much more detrimental for the trace-conditioned groups than for the delay-conditioned groups. This holds for all indices except, of course, the first avoidance-trial characteristics.

If our argument is tenable, we would expect even larger differences between the two training procedures for resistance to regular extinction, because this extinction period is characterized by a large number of CS terminations following the jumping responses. For the trace-conditioned *S*, each jump in regular extinction is *preceded* by CS termination, unless the latency happens to be less than 2 sec., while for the delay-conditioned *S*, each jump is directly *followed* by CS termination, no matter how long the jump latency happens to be. The comparison between our extinction findings and those of Kamin support this argument. The delay procedure shows extremely high resistance to regular extinction procedures. Thus, CS onset may be critical for the development of conditioned emotional reactions and the subsequent emergence of the first avoidance response, while CS termination may be critical for the reinforcement and development of instrumental avoidance responses and the attainment of the avoidance learning criterion. This interpretation is derived from Mowrer (3) and fits very well the recently published data of Mowrer and Solomon (6) and Mowrer and Aiken (4).

There is, however, one result which does not fit the theoretical argument very well, and it is a puzzler. The response latencies during regular extinction decreased in our delayed-conditioning experiment, but each CS-US group approached a different latency asymptote. Figure 2 leaves little doubt about this. Yet, since all groups are receiving the reinforcing effects stemming from CS termination after each jump, we would expect all groups to converge upon the same latency asymptote. This asymptote should be about 2 sec. One might argue that our *S*s were not given enough regular extinction trials to test this. But if we examine only those *S*s who had 200 regular extinction trials, we see the latency levels are still different across CS-US groups, though the differences are smaller than they were after 20 regular extinction trials (see Table 2). Another argument might be that CS termination produces less anxiety reduction in the long CS-US groups because these *S*s are less anxious. This was not so, however, judging from our protocols. While anxiety manifestations were more of the "gastric type" in the long CS-US groups, contrasted with more of the "lower gut type" in the short CS-US groups, there seemed to be no obvious differences in intensity of upset. Then, too, the long CS-US dogs received more shocks during training, and so they ought to show stronger conditioned emotionality than the short CS-US dogs. Yet, to say that the differential latency-of-jump asymptotes across groups reflects a Pavlovian inhibition-of-delay process does not explain the phenomenon. In addition, there is no particular feature of two-process theory which unambiguously predicts this phenomenon. Pavlovian inhibition of delay should apply to classical conditioning of emotional reactions. Should it also apply to instrumental learning?

SUMMARY

The delayed-conditioning procedure in traumatic avoidance training produces faster learning than does the trace-conditioning procedure, across a wide range of CS-US intervals. The delayed-conditioning procedure requires fewer shocks to produce the first avoidance response, requires fewer trials to reach an avoidance learning criterion, and produces greater resistance to extinction than does the trace-conditioning procedure. This superiority increases with magnitude of CS-US interval. The latency of the first avoidance response is greater as CS-US interval is increased, for both the delay and trace procedures. In addition, the asymptotic avoidance response latencies which follow the achievement of the learning criterion are longer for longer CS-US intervals; the similarity of these findings to a Pavlovian inhibition-of-delay process is noted. The quantitative features of our findings suggest that, in traumatic avoidance learning, the initial development of conditioned anxiety depends heavily on the time interval between CS onset and US onset, while the strengthening of the learned avoidance response depends heavily on the conditions of the CS termination.

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FEEDING METHOD, BODY WEIGHT, AND PERFORMANCE IN INSTRUMENTAL LEARNING

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Much learning theory is built upon interexperimental comparisons of the behavior of hungry rats, where hunger is defined, supposedly unambiguously, as time of deprivation (T_D), or number of hours since a feeding period (e.g., 3). During this feeding period, however, some experimenters (6, 7, 9, 10, 11, 14) have given each rat a limited amount of food to eat, while other experimenters (8, 12, 13, 15) have allowed each rat to eat as much as it could in a limited time. That these two feeding methods have equivalent effects upon behavior is an assumption implicit in many of the above-mentioned interexperimental comparisons and one which may account for the surprisingly large number of investigators who have neglected to state which, if either, of these feeding methods was employed. The purpose of the present study was to evaluate this assumption of equivalence by comparing the effects of the "limited amount" (LA) and "limited time" (LT) procedures upon resulting changes in body weight and subsequent performance in a simple instrumental learning situation.

METHOD

Subjects

The *S*s were 32 hooded rats, 15 male and 17 female, from the colony of the Iowa Psychological Laboratory. All were experimentally naive and between 90 and 120 days of age at the start of the experiment. Seven males and 9 females constituted the limited amount (LA) group, while 8 males and 8 females comprised the limited time (LT) group.

Procedure

All *S*s fed ad libitum from birth until the day before the experiment began. Twenty-four hours after removal from ad libitum feeding, each *S* was weighed on a Sargent Ohaus balance-type scale, and put into an individual feeding cage for its first (day 1) feeding period. Thereafter, each *S* was weighed daily immediately prior to being fed. Each *S* in the LA group found in its feeding cage 8 gm. of dry Purina Laboratory Chow, while each LT *S* found 25 gm. of the food. All feeding cages were fitted with solid plywood bottoms so that uneaten food could be saved and weighed. The feeding period lasted 50 min., after which *S*s were returned to their individual living cages. Water was always available—in the feeding cages through calibrated J-shaped drinking tubes and in the living cages from ordinary tube-stopper drinking bottles. Uneaten food was weighed following *S*'s removal from the feeding cages, and volume of water drunk estimated from the new level in the drinking tube. This procedure was repeated for 37 days, thus giving a daily record of the following measures: body weight immediately prior to eating, amount eaten during the 50-min. feeding period, and amount drunk during the 50-min. feeding period.

For the first 10 days, there was no appreciable difference in the eating behavior of the LA and LT groups since most of the LA *S*s were not eating the full 8 gm., hence were, with the LT *S*s, limited by "time" and not by "amount." After the tenth day, however, the two feeding methods became effectively different in that each LA *S* completed eating its 8 gm. while the LT *S*s, of course, could only eat a fraction of their 25-gm. allowance. By day 30, LA rats were able to ingest 8 gm. in less than 20 min.

Feeding periods for all groups began at the same hour each day until day 22, when the LA males and LT males had their feeding times moved back 1½ and ½ hr., respectively, and the time of feeding of the LA females and LT females was moved forward ½ and 1½ hr., respectively. These changes were effected in preparation for the instrumental learning trials, which required running the *S*s in smaller squads and at different hours of the day.

On days 28 and 29, *S*s were given preliminary training in an apparatus designed to measure acquisition of a learned running response (described below). On day 30, training proper of the running response began and continued until day 37. All *S*s were run under 22-hr. deprivation. Each training session lasted approximately 1 hr., following which came the daily weighing and feeding period. On day 38, all *S*s were returned to ad libitum feeding by introducing a large quantity of dry Chow into their living cages, but each *S* continued to be weighed at the same hour for seven more days.

Apparatus

The apparatus used to measure performance in instrumental learning was a modification of a particular type of Skinner box which has been described elsewhere (6, 7, 9, 10). It consisted of a small, triangular response chamber with flat-black, plywood walls and a brass floor. A starting alley led into the front apex through an outer metal door and an inner door of glass. A brass bar could be presented ¾ in. through a hole in the opposite wall. Raising the glass door started a Standard Electric Timer. By touching the bar, *S* completed a low-ampere contact relay circuit (4) between the brass floor of the box and the bar. Closure of this circuit stopped the timer, retracted the bar, and fired a Hunter Decade Interval Timer (5). One second later, a .08-gm. pellet of food dropped into a food cup situated just below where the bar had been. A 1000-cycle tone sounded concurrently with the release of the pellet and was turned off manually after *S* obtained the food. The apparatus was situated in a dark, sound-resistant room. A shielded 7-w. bulb was located above the food cup; the total illumination level in the response chamber was such that the food cup could not be seen by *E* (nor, presumably, by *S*) unless the 7-w. light above it was on.

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On day 28 and on day 29, each *S* received 1 hr. of preliminary training in order to eliminate irrelevant exploratory behavior during learning, and to establish the secondary reinforcing properties of the 1000-cycle tone. The bar was never present during this preliminary training. Each *S* was placed in the response chamber with the bar light on and a pellet of mash in the food cup. Thirty seconds after *S* obtained this food and was facing the food cup, another pellet was delivered, accompanied by the sound of the 1000-cycle tone. The tone was turned off after *S* appeared to have eaten the pellet. In this manner 6 more pellets were given at approximately 30-sec. intervals, whereupon *S* was removed from the apparatus until the following day. Preliminary training thus consisted of the receipt of 14 pellets of food, 7 per day.

Training proper began the day after preliminary training and continued every day thereafter for a total of eight days. On each trial, *S* was placed in the starting alley and the metal door raised as soon as *S* faced the response chamber; 3 sec. later the glass door was raised, permitting entrance into the response chamber. The time between the raising of the glass door and *S*'s contact with the bar was recorded to the nearest .01 sec. on each trial. A total of 72 trials was administered at the rate of 4 per day for the first three days, and 12 per day thereafter. The average intertrial interval was 5 min.

RESULTS

Daily changes in mean absolute body weight of all groups are depicted in Figure 1. The same changes expressed in terms of percentage of original (day 1) body weight are shown in Figure 2. These graphs were plotted day by day during the experiment, and day 28 was chosen for the beginning of preliminary training in instrumental learning because body weights seemed to be approaching stable values at that point.

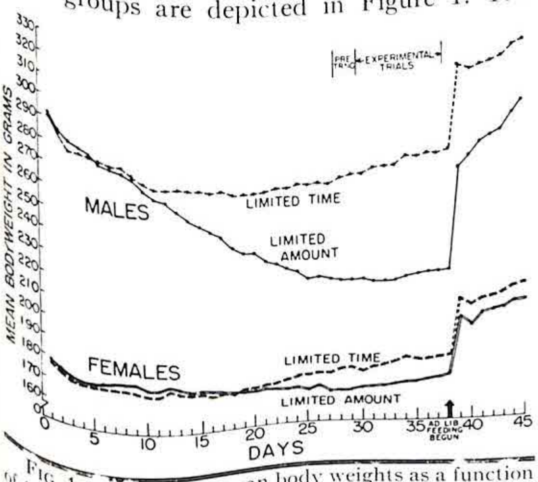

FIG. 1. Daily group mean body weights as a function of feeding method and sex.

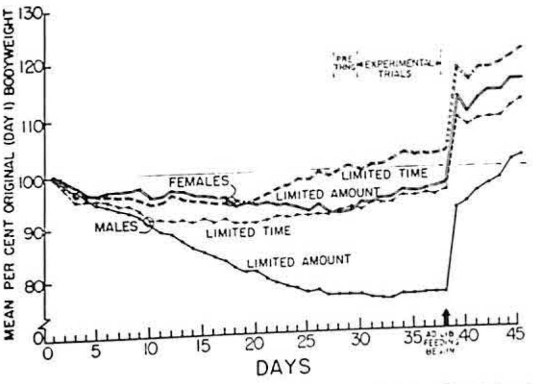

FIG. 2. Daily group mean percentages of original body weight as a function of feeding method and sex.

TABLE 1

Group Mean Body Weight Measures

Measure	Feeding Method	Males	Females
Mean body weight Days 1–8	LA	280.07	174.12
	LT	278.89	172.14
Mean body weight Days 30–37	LA	222.41	169.73
	LT	274.25	180.46
Mean % original body weight Days 30–37	LA	76.34	94.82
	LT	94.14	101.44

The following mean body-weight measures were computed for each *S*: (*a*) mean absolute body weight, days 1 to 8; (*b*) mean absolute body weight, days 30 to 37; (*c*) mean percentage of original body weight, days 30 to 37. Group averages of these means (in gm.) are shown in Table 1.

Statistical analysis indicated that the mean LA-LT body weight difference during days 1 to 8 was insignificant. By days 30 to 37, however, there were significant differences (see Table 2) between all pairs of groups but one, in both mean absolute body weight and mean percentage original body weight. These differences were more meaningfully evaluated by individual *t* tests because an initial 2 × 2 factorial analysis yielded a significant sex-by-feeding-method interaction in both the ab-

TABLE 2

Values of t Based on Differences Between Group Body Weight Means, Days 30–37

Group	Absolute Body Weight			Per Cent Original Body Weight		
	LT-M	LA-F	LT-F	LT-M	LA-F	LT-F
LA-M	6.62*	6.91*	5.35*	10.53*	11.26*	14.88*
LT-M		14.21*	12.39*		.40	4.51*
LA-F			1.46			4.21*

* Significant beyond the .001 level.

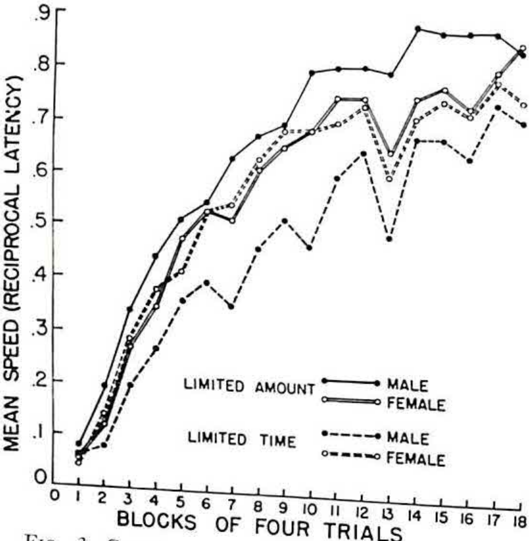

FIG. 3. Group mean speeds (reciprocal latencies) in a simple instrumental learning situation as a function of feeding method and sex.

solute ($F = 5.21$, $p < .05$) and percentage ($F = 36.31$, $p < .001$) weight measures. The two most important findings which may be abstracted from these analyses are: (*a*) LA males dropped to a significantly lower weight than did LT males, but there was no significant difference in final weight between LA females and LT females; and (*b*) although both LT groups retained a significantly larger percentage of their original body weight than did the corresponding LA groups, this superiority of the LT method was significantly greater for males than for females (as indicated by the above-mentioned significant sex-by-feeding-method interaction in the percentage weight measure).

Of the LT groups, males ate significantly more per day during days 30 to 37 than did females ($t = 5.67$, $p < .001$). Group means were 12.73 gm/day and 9.86 gm/day, respectively. (Both LA groups, of course, ate their total ration of 8 gm/day.) Measurement of amount of water drunk during the feeding period proved unreliable due to spillage, hence no analyses of this factor were undertaken.

Group mean performance curves for the instrumental learning situation are shown in Figure 3. A mean running speed over all trials was calculated for each S; group averages of these means are shown in Table 3. As in the case of the body weight measures, the speed scores revealed a significant sex–by–feeding-method interaction ($F = 6.12$, $p < .05$); consequently, group differences were analyzed by the individual t tests shown in Table 4. The most important result to be noted here is that LA males ran significantly faster ($p < .01$) than did LT males, whereas there was no significant difference ($p > .50$) between the speeds of LA and LT females. It will also be noted that of the LA groups, males ran faster than females, but among the LT groups, the reverse was true—females ran faster than males.

Correlations calculated between measures of body weight, speed, and amount eaten were, as might be expected, generally unreliable. The r's between measures of a single group, based as they were on 7, 8, or 9 pairs of observations, were variable and not significant. Correlations between measures of all Ss were either inflated or depressed by the extreme differences between sexes and feeding-method groups. For example: (*a*) the group correlations, for days 30 to 37, between amount eaten and mean percentage of original weight were

TABLE 3

Group Speed Means, All Trials

Feeding Method	Males	Females
LA	.6554	.5784
LT	.4716	.5660

TABLE 4

Values of t Based on Differences Between Group Speed Means, All Trials

Group	LT-M	LA-F	LT-F
LA-M	3.68**	1.58	1.79
LT-M		2.19*	1.95
LA-F			.26

* Significant beyond the .05 level.
** Significant beyond the .01 level.

.17 and .35 for LT males and females, respectively, but the combined correlation for both LT groups was −.56; (*b*) group correlations, for days 30–37, between amount eaten and absolute weight were .67 for LT females and .74 for LT males (neither significant), while the combined LT correlation was inflated to a significant .92.

DISCUSSION

It has been demonstrated that the LA and LT feeding methods, as defined in this experiment, do not have equivalent effects upon either body weight or running speed, and, further, that this feeding-method factor interacts with sex in both body weight and speed measures. Two obvious qualifications of these results must be stated, however: (*a*) the obtained differences clearly do not represent the effects of "limited amount" and "limited time" procedures in general but are peculiar to the values, frequently employed, of 8 gm. amount and 50 min. time; (*b*) the obtained differences in body weight (and perhaps in speed) are related most immediately to the amount of food eaten. That the LT groups remained heavier than their LA counterparts simply reflects the fact that rats can learn to eat more than 8 gm. in 50 min. One implication of these findings remains clear, however, namely, the need to specify in any definition of hunger, not only hours of deprivation, but also the method by which feeding was restricted, and for how many days, before training began.

The implications of the observed relationship between speed and body weight are, unfortunately, not as clear. No single relationship was demonstrated for both sexes. There was some indication among the males that running speed was inversely related to body weight (and thence to amount eaten) in the fact that the significantly lighter LA males ran significantly faster than did the LT males. Exploratory behavior has been found to bear a similar inverse relationship to body weight among nondeprived male albinos (1). Among the females, however, 8 gm. was apparently sufficient to maintain the LA group close enough to the weight of the LT group so that even if this inverse speed–body weight relationship holds for females, there was no opportunity to observe it.

One further relationship may be pointed out. If the mean amounts eaten by the LT groups (12.73 gm. by males, 9.86 gm. by females) may be taken as the "50-min. capacities" of the LA groups as well, then the 8 gm. eaten by the latter may be expressed as a percentage of the amount which could have been consumed. Eight grams for LA males constituted about 63 per cent of what they could have eaten, while the same 8 gm. for LA females was approximately 81 per cent of their capacity. It is interesting to note that each of these percentages is approximately the same proportion (.82 to .85) of the mean percentage of body weight retained by the group involved (76.34 per cent by males, 94.82 per cent by females). From this correspondence, it may be concluded that, despite the faster metabolic rate of males (2), percentage of original body weight retained by both sexes under limited-amount deprivation will be directly related to whatever proportion that daily amount is of their capacity. Pursuing this reasoning still further, it may be deduced that in order for the LA females in the present experiment to have lost a percentage of their original body weight equal to that lost by LA males, they would have had to receive approximately 6 gm. (63 per cent of 9.86 gm.) instead of 8 gm. per day. Since 50-min. capacities seem to be inversely related to the percentage of body weight retained by a group receiving less than its capacity daily, the following general statement may be made: If males and females are to be maintained on a daily limited amount, and if it is desired that males and females lose about the same percentage of their respective original body weights, then females should receive only 77 per cent as much food as males (9.86/12.73 = .77). This finding, if general, should be of interest to theorists who define drive strength in terms of percentage of body weight lost, and to those experimenters who prefer the LA procedure because of its more exact control of amount eaten.

SUMMARY

The present study compared the body weight changes and subsequent running speeds of two groups of hooded rats fed by different procedures: a "limited amount" (LA) method, in which each rat received 8 gm. of dry Purina Laboratory Chow daily, and a "limited time" (LT) method, in which each rat was allowed to

eat as much Chow as it could during a daily 50-min. period.

The LT groups fell to higher mean body weights than did the LA groups (significantly so for the males), and also retained significantly higher mean percentages of their original body weight. This LA-LT difference was significantly larger for males than for females in both the absolute and percentage body weight measures. LT males ate significantly more per day than did LT females.

During 72 food-reinforced speed trials under 22-hr. deprivation, LA males ran significantly faster than did LT males, but there was no significant difference between the female LA and LT groups. LA males ran faster than LA females, but LT males ran slower than LT females.

Relationships between feeding methods, body weight, and running speed were discussed. It was concluded that a definition of hunger should specify, in addition to hours of deprivation, how and to what extent feeding was restricted before training began.

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THE EFFECT OF NONREWARD AND INTERFERENCE ON VARIATION IN THE AMPLITUDE OF AN INSTRUMENTAL RESPONSE

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This paper reports the results of two investigations concerning the relation of nonreward and interference in an instrumental-act sequence to the amplitude and variations in the amplitude of instrumental behavior.

It is well known that reward, nonreward, and delays of reward (as empirical events) play important, if not crucial, roles in producing the more or less permanent modifications called learning. The present investigations, however, are not concerned with the learned consequences of reward, nonreward, or interference, but with the innate changes in the quantitative characteristics of responses which may be initiated by them.

In an earlier investigation of the effects of interference on kindergarten children by the senior author (7), it has been indicated that response strength as measured by the speed of turning a crank increases with interference. In a number of pilot studies, speed of crank-turning appeared to be decreased by nonreward. However, these effects have not been reflected immediately after the introduction of interference or nonreward but develop only after extended repetitions. Furthermore, some *S*s actually decreased in speed after extended interference and increased in speed after extended nonreward or failure. The most notable thing, however, about the individual graphic records of these *S*s has been the changes in the pattern of crank speed with the introduction of nonreward and interference. These records give the general impression that the over-all speed of crank-turning per se is to a large extent dependent on individual *S* characteristics while the degree of oscillation or stability of crank speed is affected by interference and nonreward independently of individual *S* characteristics.

The possibility is suggested that the effect of failure, nonreward, and interference is to increase the degree of behavioral variation. In this case, increases (or decreases) in over-all response strength could be regarded as an artifact. Restlessness, variation, and behavioral instability have been frequently associated with various need conditions and have been specifically noted in human *S*s as a function of failure situations in the studies of Kuhlman (3), Postman and Brown (6), and others. While there is some evidence suggesting a different relationship (e.g., 1, 4, 5), it is tempting to suppose that unreduced needs, before learning, are associated with increasing behavioral variation (in amplitude and directional and instrumental movements) and "reward stimulation" with decreasing behavioral variation. Whatever the reasons, variability is essential in most need situations requiring "new" responses, since it increases the likelihood that appropriate behavior will occur, while continued variability is a disadvantage when stimulation appropriate to reducing the need does occur. As one step in the investigation of the relation of behavioral variation to various motivational and reward conditions, the present investigation provides evidence concerning variations in the amplitude of an instrumental response (crank-turning) during extended nonreward, reward, and interference.

EXPERIMENT I

METHOD

Subjects

A total of 28 children of both sexes, between the ages of 48 and 72 months, were used as *S*s. All *S*s were attending the YM-YWCA sponsored kindergarten at the University of Mississippi.

Apparatus

The apparatus consisted of a modified version of the crank-turning apparatus described for a previous experiment (7), and was situated in a research trailer maintained by the Psychology Department of the University of Mississippi. Turning the crank lit a series of six panel lights, one at a time, proceeding from the top downward. At the sixth light, a marble was dispensed. The earlier apparatus was modified so that panel-light movement depended on the speed of crank-turning. Five revolutions of the crank were required to move the light from one position to the next. Thus, a total of 25 turns were required to obtain each marble.

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[1] The authors are indebted to Miss Katherine Easley for her capable and conscientious assistance throughout this investigation. The data of experiment I are based in part upon the master's thesis of Miss Easley (2); the data of experiment II were obtained in connection with the master's thesis of the junior author.

The time required to obtain each marble was recorded by a Standard Electric Timer which operated only while the crank was being turned. An Esterline-Angus Recording Voltmeter (maximum reading = 10 v.) produced a graphic record of the relative changes in speed of turning as reflected by voltage changes from a small A.C. generator attached to the crank.

Other materials were: (*a*) black and white marbles denoting reward and nonreward, respectively; (*b*) a wooden marble block with a movable marker for denoting when the block was completed; (*c*) a cylindrical box, placed at the feet of the *S*s, into which white marbles were discarded (*S*s could not see the marbles once they had been discarded); and (*d*) various small toys, as take-home prizes. As in previous experiments (7, 8), the recording apparatus was in a separate room from the crank box and toys.

Procedure

Each *S* completed two sessions administered on separate days, a preliminary session involving 12 training trials and an experimental session involving either 20 reward or 20 nonreward trials. For the experimental session, *S*s were paired on the basis of their mean crank speed during the preliminary session and then divided at random into two equal groups of 14 *S*s each without regard to sex. The groups were then assigned at random to the reward and nonreward conditions. Twenty additional trials involving a reversal of these reward conditions were also a part of this session. However, the results of this part of the experimental session are not relevant to the present report and will not be presented.

Preliminary session. This session was basically similar to the preliminary training procedure used in previously reported investigations involving the present apparatus (7, 8). All *S*s were required to turn the crank for a total of 12 trials on each of which the panel lights moved downward through six positions, after which a marble was received. The crank was turned out continuously throughout the panel sequence which defined each trial. During this session, black marbles were received by all *S*s on all but the second and eleventh trials, on which the *S*s received white marbles. Black marbles could be used to fill the marble board for a prize; white marbles had to be discarded into the floor container. No instructions concerning speed were given. An approximately constant between-trials interval was maintained by requiring *S* to wait for the sound of a bell before beginning the next trial. Each *S* was told that when he had put enough marbles into the groove on his marble board to fill it up to the marker, he would be entitled to choose any one of the prizes on display in the room and take it home with him.

The total time in seconds required to obtain each marble was recorded for each of the 12 trials and served as a basis for matching the groups for the experimental session.

Experimental session. The *S*s were returned to the crank-turning situation in from one to three days following the preliminary session. *S*s were told they were going to play the same marble game which they played before and were briefly reviewed concerning the crank, lights, black and white marbles, and the marble board. The *E* left the room before the beginning of the session and, as before, conversation between *S* and *E* were kept at a minimum. The marble board was marked to hold 21 marbles. All *S*s ultimately received 21 marbles. As stated earlier, the reward-nonreward conditions were reversed after 20 trials for 20 additional trials (which have been omitted from this report). All *S*s then received a final black marble, selected a prize, and were returned to the kindergarten.

The total seconds per trial and the graphic record of the voltage output from the crank were recorded for each trial. To obtain a score for the degree of range or oscillation of crank speed during each panel sequence, the difference was obtained between the highest and lowest marks (reflecting the highest and lowest crank speeds) on the Esterline-Angus record charts for each trial. This difference constituted the range or oscillation score for each *S* per trial. To avoid distortion due to occasional momentary stopping of the crank during a panel sequence, extreme low points on the charts were disregarded unless they were characteristic of the trial as a whole.

EXPERIMENT II

The purpose of experiment II was to secure data concerning the effects of additional trials of continuous reward and nonreward and the effects of interference on speed and range of response strength as measured by crank-turning.

METHOD

Subjects and Apparatus

Experiment II was administered to the same *S*s used in experiment I and began approximately two months following the completion of experiment I. Five *S*s were no longer available at this time and three *S*s had to be discarded because of apparatus difficulties. Therefore, the total number of *S*s used in experiment II was 20.

The apparatus and quantitative measures of crank speed and range were identical to those used in experiment I.

Procedure

The procedure was the same except that 40 trials of continuous reward (black marbles) or continuous nonreward (white marbles) were administered to each *S* followed by an interference condition on trial 41. The nine remaining reward *S*s and 11 remaining nonreward *S*s of experiment I were assigned to the same reward and nonreward conditions. No preliminary training was required since all *S*s were already familiar with the crank-turning situation. Each *S* was brought to and from the research trailer by the same person as in experiment I and given the same review and preliminary instructions.

The interference conditions introduced on trial 41 consisted in allowing the panel light to reach the second to the last light and then returning it to the top of the panel without a marble being received. This was repeated three successive times. Each return took 5 sec. and was accompanied by the sound of a buzzer. After the third return, the panel light was allowed to proceed downward until a marble was received as in earlier trials. At the end of this interference trial all *S*s received a black marble. So that all *S*s in both reward and nonreward groups could complete their marble board and receive a prize, the interference trial was followed by four "finish" trials on each of which black marbles were received.

Since nonreward *S*s received 40 white marbles and 5 black marbles, they were given a marble board marked for 5 marbles; the marble board for reward *S*s was marked to hold 45 marbles, which included the interference trial and four "finish" trials.

RESULTS AND DISCUSSION

A summary of the changes in mean crank speed per trial (seconds per panel sequence) for both experiments I and II is shown in Figure 1.

Mean crank speed for both the reward and the nonreward groups generally increased throughout the 20 trials of experiment I. There were no significant differences in speed between reward and nonreward *S*s in experiment I.

In the second part of Figure 1, which shows changes in mean crank speed during experiment II, mean speed for *S*s receiving reward on every trial begins somewhat higher than their speed at the beginning of experiment I and gradually increases. The approximately flat and stable trial-to-trial speed over the final 20 trials for these reward *S*s suggests a limit of speed toward which they are approaching under the particular reward conditions of this experiment. It is curious that the initial speed of these *S*s is nearly identical to their final crank speed of experiment I, which occurred two months earlier! Nonreward *S*s, receiving only white marbles during the 40 trials of experiment II, present a markedly different picture with respect to the stability of trial-to-trial mean speed and the general direction of change. After rapidly increasing their speed during the first eight trials, nonreward *S*s began showing wide variations in mean speed from trial to trial with an apparent trend toward slower turning. An analysis of variance of the 40 trials of experiment II yielded a Trials × Groups interaction variance which was significant beyond the .001 level ($F = 23.069$, $df = 39$ and 702), thus indicating significant differences in the observed trends

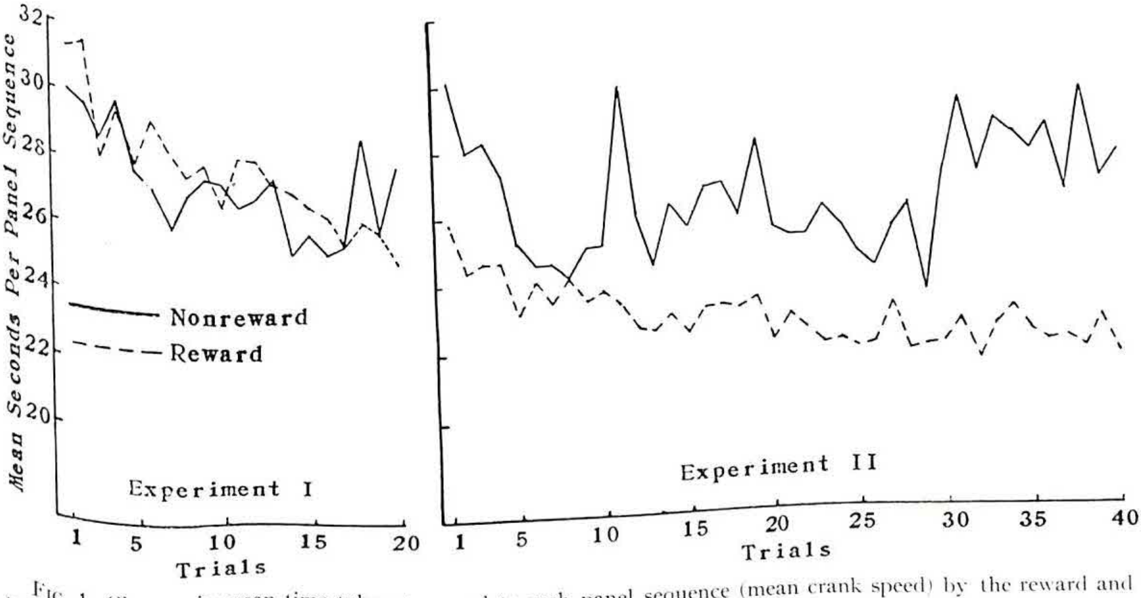

FIG. 1. Changes in mean time taken to complete each panel sequence (mean crank speed) by the reward and nonreward groups during experiments I and II.

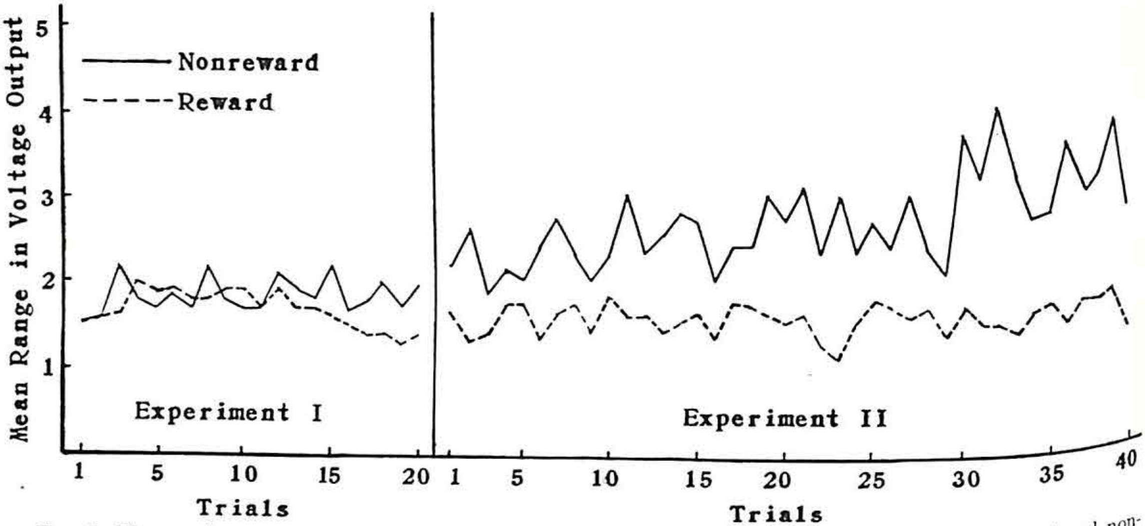

FIG. 2. Changes in range in voltage output from crank (range in crank speed) per trial for the reward and nonreward groups during experiments I and II.

for the reward and nonreward groups shown in Figure 1.

Considering the results of experiments I and II as a whole, nonreward is similar to reward in its initial effects on response strength (experiment I) but ultimately depresses mean speed per trial after extended nonreward experience (experiment II). However, it is possible that the effects of the reward trials given to all *S*s in the preliminary session may have "transferred" to the nonrewarded trials of experiment I, thus making rewarded and nonrewarded *S*s more alike in crank speed.

Figure 2 shows the mean within-trials range in crank speed (as measured by range in voltage output) for the 20 trials of experiment I and the 40 trials of experiment II. These scores represent the difference between the highest and lowest speeds reached within each of the trials as obtained from the graphic voltmeter records. The within-trials range remained about the same for reward and nonreward *S*s during the first part of experiment I, with an apparent increase for nonreward *S*s toward the end of these 20 trials. Pooling the mean scores for the final 12 trials of experiment I yielded a significant difference between the reward and nonreward groups ($t = 2.56$, $p < .03$). During the 40 trials of experiment II, the mean range scores remained consistently higher for the nonreward group. The ratio of the between-groups variance and the pooled between-*S*s variance in an analysis of various of these 40 trials yielded an F of 15.584 ($p < .002$). Although the variation between *S*s was similar for reward and nonreward *S*s, the degree of variation in the mean range scores from trial to trial was consistently larger for nonreward *S*s throughout experiment II.

It would thus appear that reward is associated with the development of less variation in crank speed during the panel light sequence and that trial to trial variation in speed remains about the same. On the other hand, nonreward is associated with significantly greater range in speed during the panel-light sequence and larger trial-to-trial variations. This greater range of crank speed under nonreward conditions is in conformity with the possibility stated earlier that reward and nonreward are related to the degree of behavioral oscillation.

A comparison of Figures 1 and 2 indicates that there is some relationship between the mean range scores and mean crank speed per trial, the slower speeds being associated with greater ranges in speed, and the faster speeds with smaller ranges. This is not surprising, since much variation of speed within trials would usually mean a sacrifice of the time required to complete the panel sequence, which would thus lower the mean speed score. Thus, the significant trend toward slower speed obtained under the nonreward conditions of experiment II (see Fig. 1) does not necessarily mean that nonreward *S*s did not at times turn as fast within each trial as reward *S*s. If they also engaged in slower turning at other times within each trial, this would lower their mean speed score and increase their range score. A comparison of the individual voltmeter records of the nonreward *S*s with those of reward *S*s substantiated this interpretation. Also, when the highest speed scores reached within each of the last ten trials by nonreward *S*s (where greatest differences in reward and nonreward crank speed occurred) were compared with the highest speed scores of reward *S*s, the difference was not statistically significant ($t = .611$, $df = 16$). Nonreward *S*s were evidently reaching as high speeds as reward *S*s. Therefore, it is concluded that the main effect of the nonreward condition in the present experimental situation was to increase the range or variation of crank speed while working for marble subgoals, and that changes in over-all response strength as measured by the time required to complete each trial is to a large extent an artifact of this former effect. It is also notable that the range scores of all *S*s in the nonreward group increased. It seems likely, therefore, that the obtained effects of nonreward on range were not greatly affected by previous environmental influences.

The effects of interference. The interference condition which was introduced during trial 41 of experiment II resulted in a sharp increase in mean crank speed and a similarly sharp decrease in range for the nonreward *S*s only. When the mean crank speed for the interference period (which comprised the equivalent of four of the nonreward trials) was compared with the mean crank speed for the five trials previous to interference, the difference for the nonreward group was significant ($t = 2.684$, $p < .03$); no significant difference was obtained for the reward group. A similar analysis of the change in the range scores also yielded a significant difference for the nonreward group ($t = 3.199$, $p < .02$) and no difference for the reward group. All nonreward *S*s increased their speed and decreased their range after interference was introduced, while the direction of change for reward *S*s was highly variable.

The lack of effects for the reward group may be due to the already high crank speed and low range in speed of this group at the time of interference. However, it is possible that the effects of any interference situation may depend upon the extent that failure has been experienced in the instrumental-act sequence. It is not possible to differentiate between these possibilities with the present data. It is rather surprising that the interference situation, which is the kind of an event that frequently is identified with other types of failure and nonreward situations, had the opposite effect on both speed and range as nonreward. Instead of "discouraging" the nonreward *S*s still further, interference appeared to have the effect that would be expected had reward been suddenly introduced. The significance of the interference condition in this experiment may have depended upon the marked change which it introduced into the general stimulus situation; the return of the panel lights plus the buzzer may have been sufficiently different from the preceding nonreward situation that it was more similar to the stimulus situation at the beginning of the experiment. In this case, the increases in crank speed and range could be regarded simply as a return to earlier behavior rather than a characteristic reaction to interference per se. Another possibility is that the novelty of the interference situation served as the innate stimulus to increasing response strength and decreasing the range in speed (8). The lack of such an effect for the reward group could be due to its already high level.

On the basis of the present data, it is not possible to evaluate these different possibilities concerning the relation of interference to response strength and variation. However, in view of the clearly different effects of nonreward and interference obtained in the present situation and the earlier investigation, it seems clear that nonreward and interference should be differentiated as experimental variables in goal-directed sequences of the present types.

SUMMARY

The purpose of these studies was to investigate the effects of extended reward, nonreward, and interference on the degree of variation in the strength of an instrumental response. Kindergarten children learned to turn a crank to obtain marbles. The faster they turned, the sooner they received a marble. One group received a black marble (reward) on every trial. The black marbles were used to fill a marble

board which was exchanged for a prize when completed. The other group received a white marble (nonreward) on every trial. White marbles could not be used to fill the marble board and had to be discarded. An interference situation which involved three successive delays in obtaining a marble was introduced at the end of this series of rewarded and nonrewarded trials. Records were kept of the total time spent turning on each trial and the difference between the highest and lowest crank speeds on each trial.

The chief results obtained were:

1. Differences in speed developed gradually, the effect for nonreward being to produce a slower speed than reward. During the early trials both reward and nonreward resulted in a similar speeding-up of crank-turning.

2. The degree of variation or range in crank speed within each trial was significantly greater under nonreward conditions.

3. The effect of introducing interference into the instrumental sequence at the end of the rewarded or nonrewarded trials was to increase mean crank speed and decrease the mean variations or range in crank speed for the nonreward *S*s only. The crank-turning of reward *S*s was unaffected by the interference condition.

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SOME EFFECTS OF PUNISHMENT AND INTERCURRENT "ANXIETY" ON A SIMPLE OPERANT[1]

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In interpreting the findings of his monumental study of punishment (5), Estes drew heavily on earlier research which indicated that conditioned emotional disturbance ("anxiety") could suppress or stop completely the output of lever responses among rats that had acquired a stable lever-pressing habit (6). He concluded that a substantial part of the initial suppressant effect of punishment on lever-pressing (with a shock to the feet) reflected conditioning of this sort (5, p. 36). The compound of stimuli (from the apparatus, etc.) which provided the occasion for lever-pressing, together with stimuli arising out of the movements of initiating and making lever responses, occurred prior to and contiguously with the punishing shocks. Through conditioning, these stimuli could acquire the power to evoke an "emotional state" which would disrupt the normal behavior of *S*, including lever-pressing, as in the earlier "anxiety" study. In support of this, Estes found that a substantial part of the suppressant effect of punishment tended to dissipate if the *S*s spent an "adaptation" period in the Skinner box, without shocks and with the lever removed.

Estes also found that punishment, particularly if intermittent, had a more specific suppressant effect which dissipated only if *S* actually made unpunished lever responses. He suggested that, with repeated punishment, withdrawal responses (R_w) incompatible with lever-pressing also became conditioned, particularly to stimuli arising from movements involved in pressing the lever.

Subsequent research has confirmed decisively the suppressant effect of conditioned "fear" or "anxiety" (following the Estes-Skinner model) on lever-pressing and other activity (1, 9, 11). But preliminary observations (1, exp. 3) early suggested that the effects of punishment and "anxiety" conditioning (the CER) differ in important details. The R_w or avoidant component in punishment appears to deserve greater emphasis than Estes' interpretation gave it. Similarly, recent discussions of punishment (4, 13) have stressed the importance of conditioned aversive properties acquired by the stimuli arising from the movements of initiating and making lever responses. Avoidant behavior, incompatible with the punished response, is thought to be positively reinforced by termination of these stimuli, while the punished response becomes increasingly unlikely to occur.

The present experiment compares a discrimination based on punishment with a conditioned "anxiety" discrimination or "conditioned emotional response" (the CER), which also suppresses lever-pressing. For both, the shocks appear only during the presentation of an arbitrary CS (a clicking noise). In punishment, the shocks are given only if and when *S* presses the lever during the CS. In CER conditioning, the shocks are given during or at the end of the CS, and no lever response is punished. In the CER, the CS acquires the power to evoke generalized emotional disturbance, as indicated by freezing and defecation. If the suppressant effect of punishment depends primarily upon the disruptive effects of emotional disturbance evoked by the CS, both groups should show an approximately equal incidence of freezing and defecation. If, on the other hand, the punishment effect depends primarily upon the development of more specific avoidant behavior, these *S*s should show a lower incidence of emotional disturbance and a higher incidence of overt behavior which has an avoidant topography. Further, the punishment suppression should dissipate rapidly as the *S*s make unpunished lever responses in the presence of the CS.

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METHOD

Twenty-two naive, male albino rats, 80 to 90 days old, were trained to press the lever in a Skinner box, first for regular and then for aperiodic water reward, available to *S* about once per minute on the average. After lever-pressing outputs had stabilized on the aperiodic schedule, the *S*s were divided into four groups, roughly equated for rate and regularity of lever-pressing, and treated as follows:

The *CER I* group ($N = 6$) received a total of nine conditioning trials during Skinner-box runs, in accordance with the standard procedure (see 11). Each trial consisted of the presentation of the CS (a clicking noise) during the fourth through the sixth minutes of a 12-min. lever-pressing run. The CS was terminated approximately contiguously with two momentary shocks to the feet (of approximately 1.5 ma. intensity), one just before and one just after the clicker went off.

The *CER II* group ($N = 5$) received a total of nine conditioning trials as above except that the shocks were introduced at the end of the first 1½ min. of the 3-min. CS in each conditioning trial. For both CER groups every effort was made, and successfully as far as could be determined, to avoid accidental coincidence of a shock and a lever response.

The *punishment I* group (P I) ($N = 6$) received a total of nine conditioning trials during Skinner-box runs. Each trial consisted of a 3-min. presentation of the clicker CS, from the fourth through the sixth minutes of the run, during which all lever responses produced a shock to the feet (approximately 1.5 ma.) through the grill floor. The shock was keyed by a microswitch on the lever and continued as long as the lever was depressed sufficiently to throw the switch.

The *punishment II* group (P II) ($N = 5$) received nine conditioning trials as given to the P I group except that only those lever responses made during the last 1½ min. of the 3-min. CS were punished.

The conditioning schedule was the same for all groups. Adaptation runs (A 1, A 2, etc.) in the apparatus, with the lever in but without CS or shocks, were interspersed among the conditioning trials (C 1, C 2, etc.) as follows: C 1, C 2, A 1, C 3, C 4, A 2, A 3, A 4, A 5, C 5, A 6, C 6, A 7, A 8, C 7, A 9, C 8, and A 10. Following A 10, the *S*s rested in the home cages for five days. Then all *S*s had two more adaptation runs followed by the last conditioning trial C 9, all with the top of the Skinner box open to permit direct observation of behavior.

On the day following C 9, all *S*s were tested for their reaction to the CS alone in the grill box. This apparatus consisted of a chamber with a grill floor, one transparent wall to permit observation of behavior, and an earphone for administration of the auditory CS (2). Afterward, on the same day, all Ss received an adaptation run in the Skinner box with the top closed.

Finally, starting on the day following the grill box test, all *S*s received a total of ten test-extinction trials (T 1, T 2, etc.) in the Skinner box with the top closed, one trial per day for ten consecutive days. Each trial consisted of the presentation of the CS, without shock reinforcement, for 3 min. at the usual time during the run.

Except during the rest period, all *S*s had a daily 12-min. run in the Skinner box, with the standard aperiodic water reinforcement schedule maintained throughout. All *S*s were on a 23-hr. water deprivation schedule during the entire experiment.

The P II procedure, with lever responses unpunished for the first 1½ min. of the CS, was included to permit the observation of the effect of the conditioning, independently of any direct suppressant effect the punishing shocks themselves might have. The CER II procedure was included partly as a rough control for P II and partly to find out whether the *S*s would discriminate the shocks as a signal that the CS no longer presaged a future shock in that trial. Not unexpectedly, it actually turned out that the I and II conditions for both punishment and CER produced neither appreciable nor statistically significant differences in behavior, with one trivial exception. The P II *S*s showed less suppression of lever-pressing than the P I *S*s during the CS on the first conditioning trial, a result to be expected as the first 1½ min. of lever-pressing was unpunished for P II but punished for P I. Accordingly, in the discussion here, the I and II P groups will be combined into a single punishment group (PUN) for comparison with a single CER group, similarly combined.

RESULTS

Figure 1 shows the effect of the punishment and CER procedures on the output of lever responses during the 3-min. period from the fourth through the sixth minute of the Skinner-box runs—the critical segment of the run during which the CS appeared.

The top panel, *A*, shows the mean outputs of the combined PUN and combined CER groups during the critical segment of the last preconditioning and the first ten adaptation trials. These curves indicate the generalization of the suppressant effects to periods in the apparatus in which the CS and shocks did not appear. At least 9 of the 11 *S*s in each group made fewer lever responses in each adaptation trial than in the last preconditioning trial ($p < .05$, for each group separately, assuming a null $p = .50$) (14). Both procedures produced a generalized suppression of lever-pressing—generalized in that it appeared in the absence of CS and shocks. The CER produced the greater generalized suppression, however. For example, the mean output for the CER group was significantly below that for the PUN group on A 1 ($t = 2.35$, $p < .05$) as well as on A 10 ($t = 2.51$, $p < .05$).

Panel *B* shows the mean outputs for these groups during presentation of the CS for conditioning trials C 1 through C 8 and for the

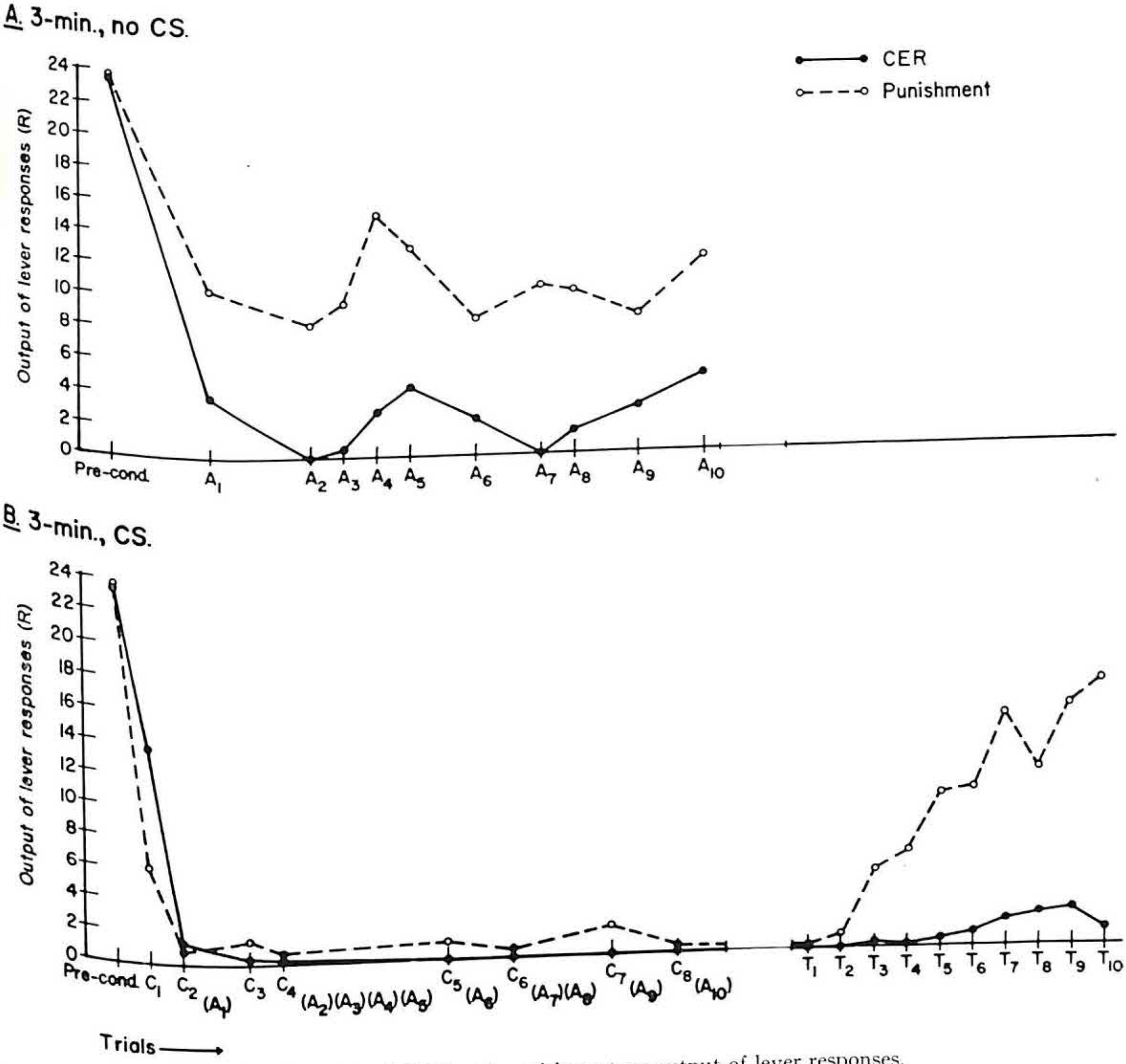

FIG. 1. The effect of CER and punishment on output of lever responses.

extinction trials T 1 through T 10 in which the CS but no shock appeared. The preconditioning output appears, again, for comparison. On trial C 2, all *S*s made fewer lever responses during the CS than they made during the equivalent segment of the last preconditioning trial. The suppressant effects of PUN and CER conditioning are obvious. But the PUN suppression was less resistant to extinction. The two groups did not differ significantly in mean output during the CS on T 1. By T 5, however, 9 of the PUN and only 1 of the CER *S*s made more responses during the CS than each had made on T 1 ($p < .01$) (8).

In trial 9, in the open Skinner box, all CER *S*s showed the usual crouching or freezing behavior during presentation of the CS. But only three PUN *S*s responded thus; the remaining eight showed at least some "abortive lever-pressing" activity. Typically, these *S*s oriented toward the lever and water cup, often placing a paw or lower jaw over the lever, occasionally depressing it slightly, then usually approached the empty water cup. Sometimes *S* simply oriented toward the lever and then went to the cup; at other times the whole sequence appeared. If *S* pressed the lever too far and gave itself a shock, it showed a mild startle response, withdrawing from the lever, usually to resume abortive lever-pressing in a few seconds. No CER *S* showed any sign of this activity while five PUN *S*s engaged in it repeatedly and continuously without any signs

TABLE 1

Incidence of Crouching and Immobility in Response to the CS during Grill Box Test*

Behavior	Group	
	CER	PUN
Crouch, no movement	9	0
Mixed crouching and movement	2	5
Normal movement, no crouching	0	6
Total	11	11

* $\chi^2 = 16.28$, $p < .01$.

of freezing, a significant difference ($p < .04$). An earlier report on punishment also has described this phenomenon (3).

In the grill box test, on the day following C 9, most CER *S*s showed the typical freezing reaction to the CS, as expected (9), while the PUN *S*s did not. Table 1 shows how the groups differed. Interestingly enough, six CER *S*s but no PUN *S*, defecated during this test ($p < .02$)

The CER group characteristically showed a higher incidence of defecation during conditioning and early in extinction. Originally the groups did not differ in this regard; on first receiving shocks in C 1, 7 CER and 6 PUN *S*s defecated. But during C 8, for example, 9 CER and 2 Pun *S*s defecated ($p <$ .01). And during T 1, when no shocks were given, 11 CER and no PUN *S*s defecated. Together with the observations of C 9 and the grill box test, these data indicate that the CS evoked more general emotional disturbance among CER than among PUN *S*s (12).

In summary, both the punishment (PUN) and "anxiety" (CER) procedures endowed an ordinarily neutral stimulus, the clicker CS, with the power to suppress lever-pressing. Both produced generalized suppression (in the absence of CS or shock) as well, with the CER procedure producing the greater generalized suppression even though no lever response had ever been punished. The PUN *S*s showed fewer signs of general emotional disturbance—they showed a lower incidence of freezing and defecation in both Skinner box and grill box. A number of them developed a characteristic abortive lever-pressing behavior not seen in any CER *S*s—an activity appearing to have clear-cut avoidant or escape components. And the suppressant power acquired by the CS was more stable for CER than for PUN in that the CER proved more resistant to extinction, as arbitrarily defined by the repeated presentation of the CS without shocks.

DISCUSSION

The relatively strong shocks so effectively suppressed lever-pressing that the PUN *S*s actually received less than half as many shocks on the average as were received by all CER *S*s (8.36 as compared with 18). Voltage control lamps in parallel with *S* blinked when *S* received each shock, permitting such a count. Perhaps the PUN *S*s showed less emotional disturbance and more rapid extinction simply because they had received fewer shocks in the presence of the CS.

But some of the major effects of the procedures appeared before the groups differed so greatly in amount of shock. By the end of C 2, all CER *S*s had received 4 shocks. By then, the PUN *S*s had received from 2 to 5 shocks, with a mean of 3.3, and 5 PUN *S*s had received 4 or more. During C 2, 9 CER and 2 PUN *S*s defecated; on the next day, during A 1, 8 CER *S*s but no PUN *S* defecated (both $p < .01$). If only those PUN *S*s which received 4 or more shocks are compared with the CER *S*s, the difference in defecation on A 1 is still significant ($p < .03$). Also, the characteristic similarities and differences in lever-pressing had appeared by C 2 and A 1.

Data already available from an earlier experiment argue more convincingly, however (10). This earlier study compared the effects of the CER I and PUN I procedures on lever-pressing, using 0.6-ma. shocks given over 6 conditioning trials. Here the PUN *S*s received from 9 to 22 shocks in the presence of the CS (with a mean of 14.25) while the CER *S*s received 12. Both procedures suppressed lever-pressing during the CS and produced some generalized suppression during adaptation runs. As in the present experiment, the CER produced the greater generalized suppression and endowed the CS with suppressant effects more resistant to extinction. The CER *S*s showed much the higher incidence of defecation. Only the PUN *S*s developed abortive lever-pressing. Each of these differences or effects was significant ($p < .05$, or better). The characteristic differences between PUN and CER conditioning appeared here even though the PUN *S*s received, on the average, *more* shocks than the CER *S*s. The results of the present experiment should not be attributed simply to the difference between the groups in the amount of shock received.

The data from the present and earlier experiments indicate that punishment can suppress lever-pressing in the absence of a general emotional disturbance sufficiently severe to produce defecation and crouching. Conditioned emotional response conditioning sufficient to have the same suppressant effects, usually entails the development of such a degree of emotional disturbance. However, the generalized suppression of lever-pressing in the adaptation trials could be interpreted to indicate that the apparatus had acquired at least some power to evoke an emotional disturbance among PUN *S*s. And the progressive increase in output during the consecutive adaptation trials A 2 through A 5 could be interpreted as showing the extinction of this effect. Also, subsequent observations in the open Skinner box have indicated that most *S*s show some crouching or freezing in response to the first few instances of punishment. Thus, some general emotional disturbance probably was evoked by the apparatus and CS in punishment, to contribute to the suppression of lever-pressing. But general emotional disturbance developed to a lesser degree than in CER conditioning and probably was not the major factor in suppressing the punished behavior. And had the CS acquired the power to evoke, by itself, a substantial emotional disturbance in the PUN *S*s, they should have showed a higher incidence of freezing and defecation in the grill box test.

Some Speculative Comments

The more rapid extinction of the punishment discrimination is not inconsistent with the emphasis by Schoenfeld (13) and Dinsmoor (3, 4) on the role in punishment of the conditioned aversive properties acquired by stimuli arising from the lever response. In the present experiment, the aversive stimulus governing the suppression of lever pressing among PUN *S*s might be a compound—the CS plus those stimuli arising from a complete depression of the lever. During extinction, the PUN *S*s would receive their full aversive compound without reinforcement each time they pressed the lever during a single presentation of the CS. For the CER *S*s, the full aversive compound—the CS plus stimuli arising from the apparatus—could be presented without shock reinforcement only once during each extinction trial. Thus a PUN *S* could have had several functional "extinction trials" while a CER *S* was having only one. Similarly, the PUN *S*s could have showed less emotional disturbance in the grill box simply because they were receiving only that part of their full conditioned aversive compound not associated with shock in the absence of lever pressing. The same argument could account also for their lower incidence of crouching and defecation in the Skinner box.

This formulation hinges upon the acquisition of aversive properties by stimuli arising out of lever pressing. In a situation employing a free operant as an indicator (7), these stimuli could not be manipulated independently of the lever response itself. Accordingly, the present interpretation must be considered tentative.

CONCLUSIONS

1. Both intercurrent "anxiety" (the CER) and punishment suppressed the output of lever responses significantly. The suppression appeared not only during presentation of the signal (the CS) but also was generalized to appear during periods in the apparatus when this stimulus was absent. This generalized suppression was significantly less severe among punished *S*s, however.
2. The suppression produced by punishment disappeared more rapidly than that produced in the CER, as a function of the repeated presentation of the CS without reinforcement by shock.
3. The punished *S*s consistently showed a lower incidence of signs of general emotional disturbance (defecation and immobility) than CER *S*s. Further, in the presence of the CS, the punished *S*s tended to show abortive lever-pressing activity, with withdrawal or avoidant components, while no signs of such behavior appeared among CER *S*s.
4. The suppressant effect of punishment here did not appear to depend exclusively, or even largely, upon the evocation of a general emotional state or disturbance by the CS, as exemplified in the CER, though such an emo-

tional reaction may have been present in a degree to contribute somewhat to the total suppressant effect.

5. Rather, the results were interpreted as consistent with the view that the effects of punishment depend heavily upon specific aversive conditioning in which stimuli arising from the punished response itself became a significant and critical part of the compound conditioned aversive stimulus which governs the suppression.

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STUDIES IN THE NEUROPHYSIOLOGY OF LEARNING: II. EFFECT OF BRAIN STIMULATION DURING BLACK-WHITE DISCRIMINATION ON LEARNING BEHAVIOR IN THE WHITE RAT

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The theoretical framework (2) underlying the present series of experiments posits two neurophysiological variables as being fundamental to the learning process: (*a*) the repetition rate or frequency of nerve impulse volleys, and (*b*) duration of the volleys. If the response to a given stimulus is mediated in the central nervous system by impulse frequencies of a given value rather than another, this fact will influence the strength of the response on successive future applications of the same stimulus. Similarly, if the duration of the impulse volleys involved in the response is of one value rather than another, the strength of the response on successive future applications of the identical stimulus will be altered accordingly. This means that the value of these two parameters would determine, in the event a muscular response were involved, whether the vigor and latency of the contraction would become, respectively, greater and shorter with successive applications of the stimulus, or, on the other hand, weaker and longer (1). At the appropriate ventral roots the phenomenon would manifest itself as either (*a*) an oscilloscopic deflection increasing with each successive application of the stimulus and diminishing in latency, or (*b*) as a diminishing deflection with increasing latency. To determine whether the effect of repetitive application of a fixed stimulus will lead to an increasing or a diminishing function in the "strength" of the response is the essence of learning theory.

Let

R = some acceptable measure of reaction or performance;

S = some acceptable measure of the amount of past stimulation, training or experience under defined experimental conditions;

ϵ = a parameter reflecting the repetition rate of the presynaptic impulse volley, the duration of the volley, and individual differences.

Then, if we write

$$\frac{\Delta R}{\Delta S} = \frac{\epsilon}{S} \tag{1}$$

this expression reflects, at least to a first approximation, the empirical findings in learning experiments. It will be noted, however, that the quotient may be positive or negative in accordance with the sense given to ϵ. This is consonant with experimental data, for in extinction, for example, the accumulation of stimulation or experience results in continuing diminution of the value of R. Any acceptable neurophysiological learning theory should account, therefore, on the basis of acceptable physiological evidence, or at least by means of hypotheses which do not outrage neurophysiological experience, for the variation in size and sign of the value ϵ under various experimental conditions.

Let

$$\epsilon = \int (af - e^{bft})\,dt \tag{2}$$

where

a and b are constants;

f = repetition rate of the presynaptic impulse volley;

t = duration of the presynaptic impulse volley.

This expression for the value of ϵ has only heuristic value, since it was not deduced from biochemical considerations. It will be noted, however, that the repetition rate of the presynaptic impulse volley, together with the duration of the volley, will determine the size of ϵ as well as its sign. Thus, for a given impulse frequency, there will exist values of t such that the integral will assume values varying from a maximal positive number to negative numbers of varying size. Equation 2, therefore, describes a parameter which summarizes and represents the neurophysi-

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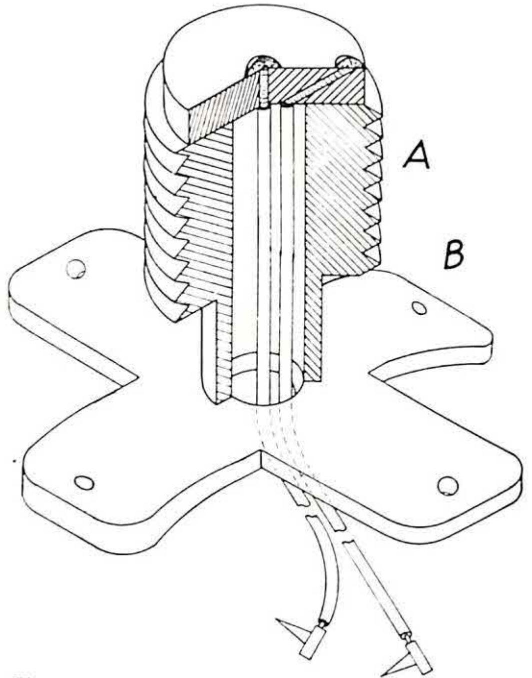

FIG. 1*a*. Permanent mounting on animal's back. *A*, "smokestack" which couples with the crystal container; *B*, platform sewed onto back muscles by means of silver wire. The mounting is made of silver; the insulating disc at top of "smokestack" is of a light plastic material and fixed in place by cement.

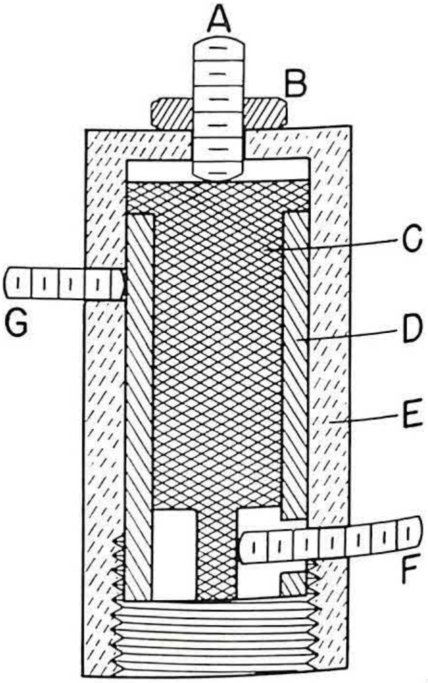

FIG. 1*b*. Crystal container. *A*, threaded bolt to which antenna is coupled, the lower end of bolt pressing against crystal *C* (1N23B); *B*, tightening nut; *D*, duralium cylinder; *E*, Lucite container; *F* and *G*, metal probes, to test contact.

ological basis for "re-enforcement." When ϵ is positive, reinforcement exists and learning takes place; when ϵ is negative, reinforcement is lacking and extinction occurs.

One purpose of the present series of reports is to present experimental evidence bearing upon equation 2; we hope to show that repetition rate of brain stimulation and duration of the volley do, in fact, affect the parameters of learning curves in a characteristic manner.

METHOD

Apparatus

Electronic. The details of the transmitter system and the reception unit worn by the animal have been described elsewhere (3, 5). There has been one change in the receiver unit in the intervening period; this is shown in Figure 1*b* and is constituted of the elements lettered *F* and *G*. These elements were developed to give assurance that when the crystal container is screwed onto the "smokestack" worn by the animal (Fig. 1*a*), electrical contact is made between the elements in the crystal container and the contact points in the "smokestack." Since the resistance of the crystal is known and can be measured across the two elements in question, effective contact with the contact points by the crystal container will serve to add another circuit in parallel (provided by the leads to the animal's brain) and thus noticeably diminishes this resistance. Thus, before the animal is placed in the discrimination box, the crystal container is screwed on and the resistance across the elements is determined by a vacuum-tube voltmeter. If this resistance equals the resistance of the isolated crystal, contact has not been made.

Surgical. This has been described earlier, and no modifications have been made (3, 4).

Discrimination box. The ground plan and dimensions of the learning unit used are given in Figure 3. It was decided to employ a black-white discrimination problem because of the greater simplicity of the behavior involved as compared to that entailed in learning a maze (4). The center compartment of the end box was painted white, while the two side compartments were painted a dull black; the starting box and runway were painted gray. The top of the unit, from starting box to end units, was covered by Lucite to permit complete visibility of the animal's behavior and to avoid electromagnetic shielding. The doors in the discrimination unit were also of Lucite and of the guillotine type. These were controlled from outside the Faraday cage by means of strings.

Procedure

Adaptation period. For approximately two weeks before the beginning of the adaptation trials in the discrimination box, the rats were placed on a 23-hr. hunger drive and were fed only the Friskie pellets which were to be used in the experiment proper. The animals were

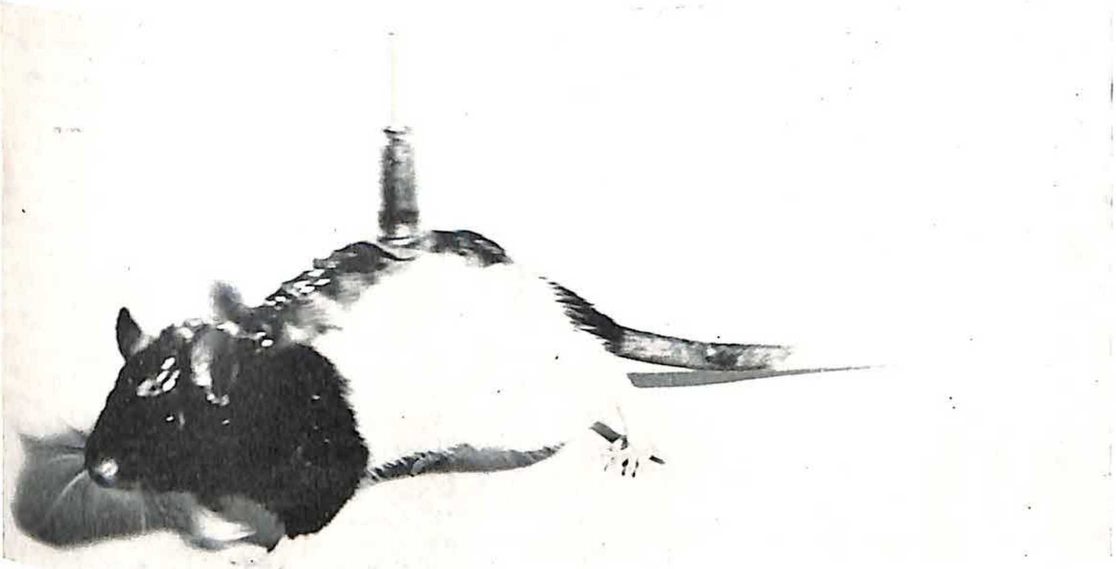

FIG. 2*a*. Crystal container and attached antenna screwed onto smokestack. The antenna in this picture is not the one usually employed, which is a tightly wound helix, suitably tuned (3, 5).

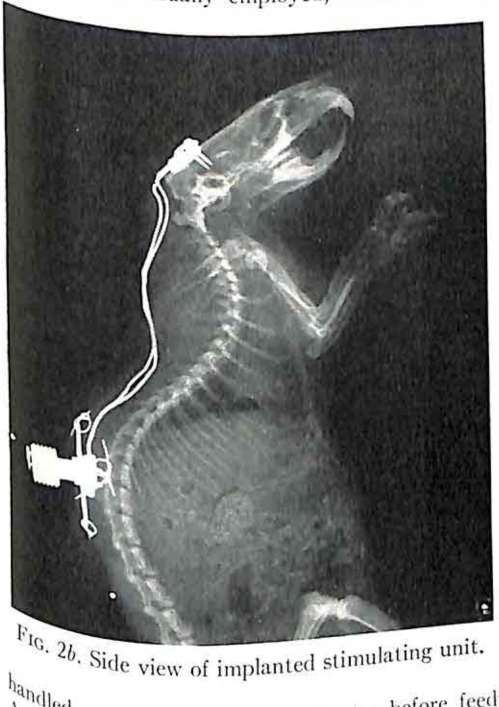

FIG. 2*b*. Side view of implanted stimulating unit.

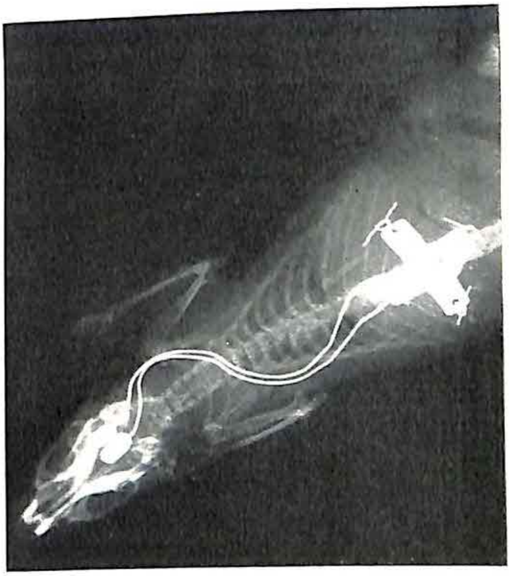

FIG. 2*c*. Top view of implanted stimulating unit.

handled each day for several minutes before feeding. At the end of this two-week period, the animals were not fed for 47 hr., after which time they were permitted to explore the discrimination unit. A gray two-compartment box was used for the purpose, with pellets placed in the cup of each compartment. The rats explored the unit, with all doors open, and in groups of threes and fours, being permitted to remain for 1 hr. The animals were not fed in the home cages, but found their daily ration in the compartments. This procedure was observed for three days. Thereafter, the rats were given, singly, two trials for one day, then four massed trials on each of four days. When *S* entered a compartment, the guillotine door was closed behind it, and it remained until the pellets (four) were eaten or for 10 min. Animals were given the remainder of their daily ration in the home cage 20 min. after the last run. Eight rats were started in each experiment, which was replicated until a sufficient *N* was secured. Animals which at the end of the adaptation period were not running briskly out of the starting box and into the goal boxes were discarded. The remaining animals were randomly divided into four groups: (*a*) normal control (NC), (*b*) operated control (OC), (*c*) low frequency

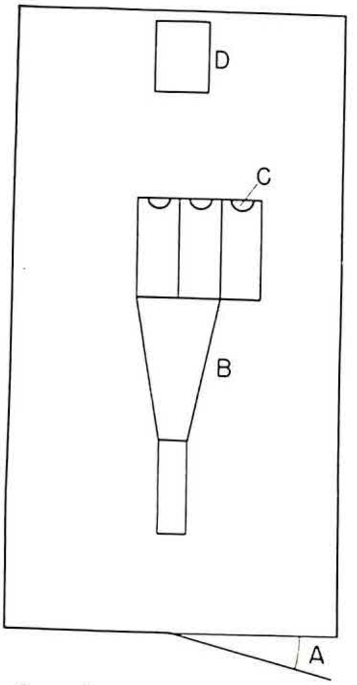

FIG. 3. Ground plan of the discrimination unit within the Faraday cage. *A*, entrance door to cage; *B*, starting box and choice-point region; *C*, food cups; *D*, oscillator. The discrimination unit was throughout 8 in. deep. Dimensions of cage, 10 ft. by 5 ft. by 5 ft. All objects in cage are drawn to scale.

(LF), and (*d*) high frequency (HF). Following the surgery, two days were allowed for recovery. On the first of these two days, the animals were put into the discrimination unit, singly, with all doors open, and allowed to eat ad libitum in either of the two compartments of the gray goal box. On the second day, the rats were given two runs each day, with two pellets as reward in either of the food cups; the door was closed as soon as the animal entered the compartment. The three operated groups (OC, LF and HF) wore the receiver unit and the attached antenna on both days, and all the maneuvers subsequently to be used with these operated rats in the test experiment were executed.

Test period. The experiment proper began on the third day after the surgery. The black-white discrimination box was substituted for the gray box used for the adaptation period. The white compartment was the re-enforced compartment. Ten massed runs were given daily, for a period of five days; the rewarded (two pellets) compartment was randomly placed on the right on five runs, and the left on five runs.

The four groups of animals were handled as comparably as possible. The three operated groups, of course, were necessarily subjected to a slightly different routine from that of the normal controls. The animal was taken from its individual cage, and the receiver unit screwed on; then the electrical test for continuity was made by measuring the resistance across the elements *F* and *G* shown in Figure 1*b*. This could be done by cradling the animal in the crook of one arm and applying the probes with the other hand, a maneuver requiring but a few seconds. This was done for rats in the OC group as well as those in the LF and HF groups. When the electrical continuity test had been made, the animal was placed in the starting box; *E* closed the door of the Faraday cage and took his place near the power switch and the pulley cord controlling the exit door. As soon as the animal entered the runway from the starting box, the oscillator was turned on. When the animal entered the correct compartment, the door was closed at once and the power turned off; the rat then remained in the reward box until it had finished eating the two pellets of food in the cup, and in any case, for a period of 25 to 30 sec., at which time it was picked up for the next run. If it chose the incorrect compartment, the door was closed behind *S*, and the power left on for 25 sec. At the end of this time the power was turned off, and the animal returned to the starting box for the next run. The animals were given their daily rations in the home cage 20 min. after the last run.

The OC group was not stimulated at all; the LF group was stimulated at 75 pulses/sec. and the HF group at 300 pulses/sec. The pulses were rectangular and ca. .75 msec. in duration. The power level was the same for the two stimulated groups, and sufficiently low as not to cause an overt reaction on the part of the animals. The power level constituting the somatic response threshold had been established on the basis of much previous experience. On occasion when a rat did show signs of muscular response, the level was lowered for it.

Effect of asymmetrical electromagnetic field. In a previous experiment it had been found essential that the strength of the electromagnetic field inside the Faraday cage be symmetrical on either side of the runway to the end boxes. In the experiment in question the position of the oscillator vis-à-vis the discrimination unit was such as to make the field on the right side of the runway and choice-point area slightly stronger than on the left. Under these conditions it was found that the animals stimulated at the high frequency manifested *persistent position habits to the left*. The low-frequency group was not affected. The normal control group was, of course, not affected; nor were the operated control animals. In order to assure ourselves that the idiosyncrasy was, in fact, due to asymmetry of the field, the position of the oscillator was shifted in such wise that the field to the left of the midline of the Faraday cage was made somewhat stronger than on the right side. Now it was found, utilizing a new group of animals, that the high-frequency rats manifested a *marked right position habit*. A test on a low-frequency group was not made.

It is interesting to note that in these preliminary experiments the animals were shying away, so to speak, from the stronger field, but that there was no overt behavioral sign that they were being "pushed." The influence of the field asymmetry was deduced from an analysis of the percentage of choices to the right and left goal boxes over each of the five days of the learning period.

It is to be emphasized, therefore, that every effort was made to keep the field symmetrical, and analysis of the data in the experiments reported here showed that no position habits were manifested for any of the four groups of animals on any of the five days of the test period.

RESULTS

Total Scores

Each rat was given 10 runs per day for five days on the black-white discrimination unit. Thus, the total number of incorrect choices or errors for each rat could vary between zero and 50. In Table 1 are given the total error scores for each animal in each of the four groups, together with the variances. The scores are arranged from highest to lowest within each group. It will be seen that the OC and the HF group have means with the maximum discrepancy, while the means of the NC and the LF groups differ hardly at all. An analysis of variance based on the method of medians (7, p. 398) gave a χ^2 of 5.48, with 3 *df*, whereas for 3 *df* $\chi^2_{.90} = 6.3$. Application of the same test with the LF group omitted (since this group is indistinguishable from the NC group) yielded a χ^2 of 5.96, whereas with a 2 *df*, $\chi^2_{.05} = 5.99$. Thus significance at the .05 level is barely missed. When an analogous comparison is made between the OC and NC groups, a χ^2 of 2.87 is obtained; for 1 *df* $\chi^2_{.10} = 2.706$. A comparison of the OC and HF groups yields a χ^2 of 3.78; for 1 *df* $\chi^2_{.05} = 3.841$.

Thus when the total number of errors made over the five-day period is utilized, statistical significance is barely missed. One cannot help but feel, however, that a significant difference would have been obtained between the OC and the HF groups had larger *N*'s been at hand. Indeed, the gross behavior of the animals while in the discrimination unit strongly supports such a supposition; the behavior of the OC rats was typically less "alert" and more sluggish than that of the HF and LF groups.

Performance as Related to Time

The number of correct choices in the ten runs given each day were averaged for each group. The resulting data are shown in Table 2, and plotted in Figure 4. Groups OC and HF are perceptibly different throughout the five days, with HF consistently superior. On the other hand the NC and the LF groups are as consistently indistinguishable throughout the same period. It will be noted, further, that

TABLE 1

Total Number Errors in 50 Choices (10 per Day) Made by the Four Groups of Rats

	OC	NC	LF	HF
	2	3	1	2
	3	3	3	3
	6	3	4	4
	12	4	6	5
	14	7	6	6
	16	8	7	7
	17	8	8	7
	18	9	9	9
	19	10	9	10
	21	12	11	11
	22	13	17	12
	24	20	23	16
	24	27	26	19
		29	27	23
		33	30	27
m	15.23	12.60	12.66	10.73
s^2	56.75	106.57	91.85	55.78
N	13	15	15	15

TABLE 2

Average Number of Correct Choices per Day (out of 10) for the Four Groups of Rats

Day	OC	NC	LF	HF
1	4.9	5.4	5.3	6.4
2	5.5	6.5	6.9	7.4
3	7.7	8.2	8.0	7.8
4	8.0	8.7	8.4	8.8
5	8.7	8.7	8.8	9.0

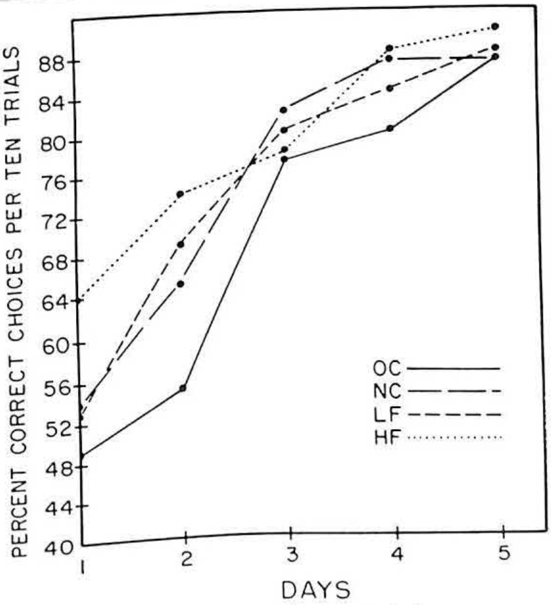

FIG. 4. Percentage of correct choices.

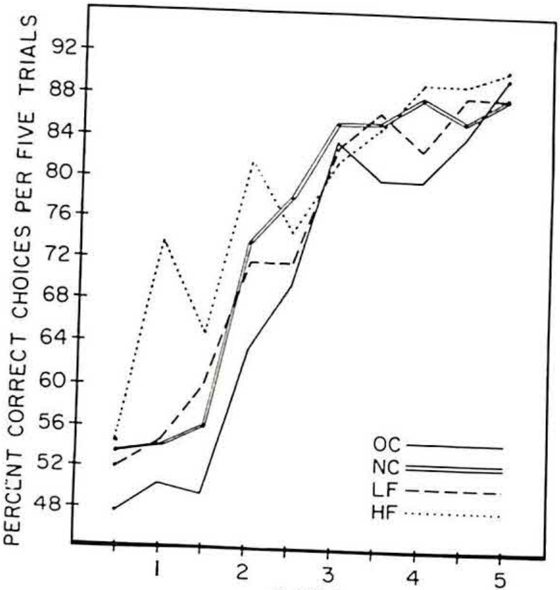

FIG. 5. Curves of learning based on five-trial units.

TABLE 3
Cumulative Averages (Every Five Runs) of Correct and Incorrect Choices for the Four Groups

OC		NC		LF		HF	
E	C	E	C	E	C	E	C
2.6	2.4	2.3	2.7	2.4	2.6	2.3	2.7
5.1	4.9	4.6	5.4	4.7	5.3	3.6	6.4
7.8	7.2	6.8	8.2	6.7	8.3	5.3	9.7
9.6	10.4	8.1	11.9	7.8	12.2	6.2	13.8
11.1	13.9	9.2	15.8	8.9	16.1	7.5	17.5
11.9	18.1	9.9	20.1	9.8	20.2	8.4	21.6
12.9	22.1	10.6	24.4	10.5	24.5	9.1	25.9
13.9	26.1	11.2	28.8	11.4	28.6	9.6	30.4
14.7	30.3	11.9	33.1	12.0	33.0	10.1	34.9
15.2	34.8	12.5	37.5	12.6	37.4	10.6	39.4

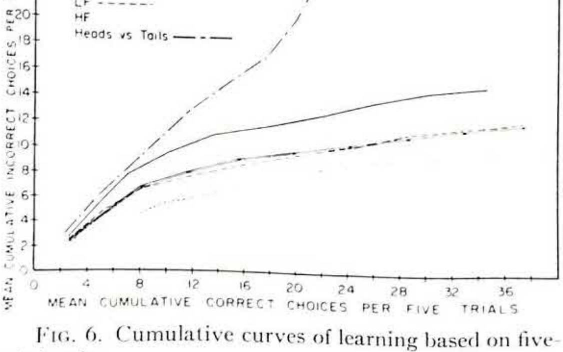

FIG. 6. Cumulative curves of learning based on five-trial units.

by the third day all four groups have reached quite comparable performances. It is interesting to note that the HF group is superior to the OC group on the very first day; this superiority lies almost exclusively in the second five of the ten runs for the day. On the first five runs the difference is approximately 6 per cent.

The curves drawn on the basis of a five-run breakdown are given in Figure 5. The first five runs of the day are given in the first half of the abscissa unit; the second five runs in the second half. Thus, between the two halves of a given daily unit the elapsed time is of the order of minutes, whereas between the second half of one day and the first half of the next there elapsed almost 24 hr. Figure 5 is presented primarily to indicate the curious serrations in the curve for the HF group during the first three days. This phenomenon drew attention because it had been observed in preliminary experiments. In both instances it appeared most clearly in the HF group.

While no attempt will be made to treat statistically the data illustrated in Figure 4, they are clearly suggestive of the processes underlying the total-score results given in Table 1. The OC is the slowest learning group, and the HF the fastest. The NC and the LF are indistinguishable in their learning rates, but both are superior to the OC group. Thus, surgery as such decelerates the learning process, but the LF group which, of course, is operated, does as well as the normal.

Ratio of Cumulative Incorrect to Correct Choices

It is of interest to plot the cumulative average number of correct choices against the cumulative average number of incorrect choices. This was done for every five runs; thus the co-ordinate values of the first point in each curve sum to 5; the co-ordinate values of the second point sum to 10; the third, to 15; etc. (6). The results are shown in Table 3 and Figure 6. The fifth curve represents the results of tossing 15 coins and cumulating the average number of heads and the average number of tails for every 5 throws until 50 throws had been made.

Here it is seen very clearly that the LF and the NC groups are indistinguishable and occupy a position almost halfway between that of the OC and the HF groups. The curves for the four groups of animals were so stable that it was decided to derive equations for them. If we express the number of cumulative errors on the y-axis and the number of cumulative correct choices on the x-axis, then the most general statement which embodies the relation between the two variables in quantitative form is the derivative

$$\frac{dE}{dC} = \frac{k}{C}, \tag{3}$$

where E is the average number of incorrect choices, C is the average number of correct choices and k is a constant. The equation asserts that the ratio of the increase of errors to correct choices becomes smaller and smaller as we go out on the x-axis. Integrating,

$$E = k \log C + K, \tag{4}$$

where K is a second constant.

Utilizing the method of least squares, the parameters k and K were calculated for each of the four groups. The equations are, respectively,

$$k = \frac{\left(\sum_{i=1}^{N} E_i\right)\left(\sum_{i=1}^{N} \log C_i\right) - \sum_{i=1}^{N} E_i \log C_i N}{\left(\sum_{i=1}^{N} \log C_i\right)^2 - \sum_{i=1}^{N} \log^2 C_i N} \tag{5}$$

$$K = \frac{\sum_{i=1}^{N} E_i - k \sum_{i=1}^{N} \log C_i}{N} \tag{6}$$

where N is the number of points on the curve (i.e., 10), E_i is the number of cumulative errors at point i on the curve, and C_i is the number of cumulative correct choices at that point. The values of k and K for the four groups are given in Table 4. The accuracy of fit is shown in Figure 7.

It is hardly worth while to raise the question of reliability regarding the set of four curves. Whatever shortcomings exist in the data are likely to be of a systematic rather than of a sampling nature. However, as a point of methodology, the following procedures are described for the purpose of determining the similarity of two empirical curves when only the co-ordinates of the points are given. No attempt will be made here to give proof.

TABLE 4

Parameters for the Curves of Best Fit for Each of the Four Groups

	k	K
OC	11.132	−1.909
NC	8.856	−1.559
LF	8.787	−1.500
HF	7.617	−1.845

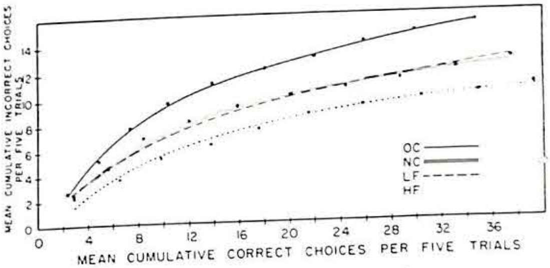

FIG. 7. Theoretical curves based on the parameters given in Table 4. The obtained empirical values are shown for three of the groups.

Let there be two sets of data a and b embodied in the graphs a_g and b_g. Determine the mathematical function of best fit for each of the two graphs and calculate the necessary parameters for each. Let the corresponding mathematical functions be termed, respectively, a_f and b_f. Then calculate the values for the dependent variable in set a by means of the mathematical function a_f and let these be named Y'_{iaa}. Similarly, calculate the values for the dependent variable in set b by means of the mathematical function b_f, and let these be named Y'_{ibb}. Compute the variance of estimate for set a, namely,

$$\sigma^2_{est(aa)} = \frac{\sum_{i=1}^{N} (Y_{ia} - Y'_{iaa})^2}{N}$$

and for set b,

$$\sigma^2_{est(bb)} = \frac{\sum_{i=1}^{N} (Y_{ib} - Y'_{ibb})^2}{N}$$

where N is the number of points in the graph. Interpreted in the context of the present investigation, Y'_{iaa} is the ith cumulative *error* score in group a predicted from the ith cumulative *correct* score in group a by utilizing its own "regression equation," i.e., $Y'_{iaa} = k_a \log C_{ia} + K_a$. Analogously, $Y'_{ibb} = k_b \log C_{ib} +$

K_b. If the ratio $\sigma^2_{est(aa)}/\sigma^2_a$ is not sufficiently small—say, somewhere between .01 and .10—the mathematical function does not fit the data very well, and legitimate doubts may be raised regarding its usefulness. Similarly, as regards the ratio $\sigma^2_{est(bb)}/\sigma^2_b$.

If the mathematical functions a_f and b_f fit their respective data satisfactorily, we proceed to determine whether the two functions are significantly discrepant. Let

$$s^2_{est(aa)} = \frac{\sum_{i=1}^{N} (Y_{ia} - Y'_{iaa})^2}{df}$$

be an unbiased estimate of the mean square discrepancy, calculated for many replications of the experiment, between the actual values in set a and those predicted for it by the corresponding mathematical function a_f. Analogously, let

$$s^2_{est(ba)} = \frac{\sum_{i=1}^{N} (Y_{ib} - Y'_{iba})^2}{df}$$

be an unbiased estimate of the mean square discrepancy, calculated for many replications of the experiment, between the actual values in set b and those predicted for it by the mathematical function a_f, where $Y'_{iba} = k_a C_{ib} + K_a$. That is to say, the cumulative correct scores in experiment b are used for predicting the cumulative incorrect scores in that experiment, but the parameters derived from experiment a are substituted in the equation. If the two mathematical functions a_f and b_f are comparable to an acceptable degree, then the actual values in set a and those in set b will be predicted equally well by mathematical function a_f. Similarly, the two sets of actual values would be predicted equally well by mathematical function b_f. An index of the discrepancy between the two empirical curves is provided by forming the ratio

$$s^2_{est(ba)}/s^2_{est(aa)}$$

This ratio, in the null case, will be distributed as F with the appropriate degrees of freedom. In the context of the present report $df = N - 2 = 8$, since two parameters are involved in the mathematical function used.

In the present experiment, all comparisons except that between NC and LF were significant at beyond the .01 level. The NC and LF comparison is significant at slightly less than the .20 level. From this we conclude that the OC group was the slowest to form the discrimination habit, and the HF group the fastest. The NC and LF groups were indistinguishable one from the other and were located roughly halfway between these two extreme groups. From these results we draw the tentative inference that speed of formation of light-dark discrimination habit is increased by both repetition rates, but more by the fast than by the slow.

DISCUSSION

In these experiments the black-white discrimination habit was made the object of study because of the relative simplicity of the behavior involved. In an earlier investigation (4), a three-unit maze was used, but individual differences were so great that the animals were all trained in a given maze pattern prior to the surgery and were subsequently made to run in a reversal of the original pattern while stimulated. Although this maneuver insured perhaps a greater homogeneity among the rats at the start of the experiment proper, it made interpretation of the results difficult, since learning involved not only the acquisition of a new pattern but the breaking of an old one which was recently and fairly firmly established. The results obtained with the discrimination box are certainly easier to interpret.

A factor which would be in the nature of a systematic error in this study is the possibility that the brain stimulations actually produced pain reactions—"hurt" the animals—and that the amount of nociception was a function of the repetition rate of the applied brain stimulation. Thus the HF group, if this were true, would be hurt more than the LF group, and the 25-sec. delay with the power turned on when the incorrect box was chosen would merely serve as a more intense "punishment" for the HF group than for the LF. Thus, the better performance of the former group would merely illustrate that degree of punishment relates to speed of learning.

This possibility was kept in mind from the very onset of the series of experiments, and every effort was made to obviate it by keeping the power level of the field sufficiently low as to evoke no overt behavioral reaction, and yet no lower than necessary. Careful observation of the animals while running to the choice compartments and while waiting therein during the delay interval revealed no indications of stimulation except in rare instances. The fact that the electrodes penetrated 1 to 2 mm. into the cerebrum (Fig. 2) and were insulated except for about 1 mm. at the tip lends credence to the belief that probably no receptors were stimulated

While the results expressed (*a*) as total errors are not statistically significant and (*b*) as errors per day, are probably not significant, they both suggest that the HF group improved most rapidly and the LF group next, the speed of learning in the latter being such as to make its performance equal to that of the normal control group. It remained for the statistical treatment utilizing "cumulative incorrect-correct runs" to bring out clearly what was merely indicated by the other statistics (6). The results expressed in this fashion are so stable and consistent that it is difficult to dismiss them as artifactual, particularly in view of the fact that it was possible to fit a mathematical function to each with a satisfactory $\sigma^2_{est}/\sigma^2_{tot}$ ratio. For the OC group this was .005; for the NC group, .003; for the LF group, .004; and for the HF group, .028.

If we give the results reported here tentative acceptance, we have some evidence that the repetition rates of the impulse volley traversing the synaptic systems in the cerebral mass has a bearing on the rate of the learning process. One objective of these series of experiments is to show that, for a given duration of the impulse volley, the value of ϵ in equation 2 varies as some direct function of the repetition rate, provided the rate does not approach the limit of relative refractoriness. What is required, therefore, are series of experiments such that a whole spectrum of frequencies is tested. We should, in light of the hypothesis, expect a family of curves similar to those shown in Figure 6, the lowest frequency being at the top and indistinguishable from the OC group, and the highest frequency at the bottom.[2]

Analogously, series of experiments are required in which the frequency of the impulse volley is fixed but its duration altered systematically from a minimum to some upper value. We should then expect a family of curves whose level would vary as a rather complex function of the duration. Depending on the frequency used, the curve heights might very well diminish as the duration increased up to some value of the time, and increase thereafter, to the limit of random choice.

It would seem, however, that to explore systematically the various combinations of repetition rates and volley durations will require a type of behavior that is even simpler than that offered by the discrimination box. Possibly a suitable adaptation of the Skinner apparatus will serve the purpose.

SUMMARY

1. An experiment is described in which the cerebrum of the white rat is stimulated while the animal is in the process of forming a black-white discrimination habit.

2. Two repetition rates, one of 75/sec and the other 300/sec, were used. Evidence is presented that both the higher and lower frequencies accelerate the rate of forming the habit, with the higher frequency giving the greater effect.

3. A sketch of the theoretical framework, neurophysiological in nature, underlying the experiments is given; the results reported lend tentative support to the hypothesis advanced.

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[2] When a Gulliksen-type of analysis is used, the parameter k in equation 4 becomes inversely related to the parameter ϵ in equation 2.

TIME ERROR IN TACTILE SIZE JUDGMENT AFTER PENETRATING BRAIN INJURY[1]

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Most studies of sensory function after cerebral lesion are concerned with changes in sensitivity irrespective of temporal relations between stimuli. However, significant changes in function may be revealed if one studies the temporal course of sensation and the interaction of multiple stimuli in time. Such studies are rare, especially in work on subhuman primates. One exception is the delayed response test, in which duration of interpolated delay is the crucial variable in demonstrating inferiority of monkeys with bifrontal lesions to those with other brain lesions.

In an earlier study (6), the author has demonstrated that successive comparison of weights results in greater negative time error (overestimation of the second of two equal weights) in men with parietal lesion as compared with a control group without brain injury, or a group with brain injury exclusive of the parietal lobe. In this study it was also demonstrated, for the first time, that the negative time error for weight judgment obtained on unilateral stimulation (i.e., either hand alone) significantly exceeds that obtained on bilateral stimulation (i.e., both hands).

Further investigation of the problem of time error in size judgment was undertaken since deficits in size and weight discriminations were earlier shown to be dissociable after brain injury (4, 5). The objectives of the present study were threefold: (*a*) to determine the normal time error as a function of duration of interpolated time, and of unilateral or bilateral stimulation, (*b*) to compare the effects of locus of brain lesion, and of somatosensory status following brain injury on the time error, and (*c*) to compare the results with those reported earlier for weight judgment.

METHOD

The *S*s, apparatus, and procedure are described in detail in earlier studies of weight and size discrimination (4, 5, 6), and are summarized below.

Subjects

There were 30 brain-injured *S*s and 30 control *S*s without brain injury. Half the brain-injured group had evidence of somatosensory impairment of the hand; of the control group, half had injury to the peripheral nerves supplying the hand, the other half, injury to the peripheral nerves of the leg.

Division of the 30 brain-injured *S*s was also made on the basis of the lobe injured, e.g., the group was divided into those with injury to the frontal lobe, and those with brain injury exclusive of the frontal lobe. The group was similarly subdivided for the other lobes. For analyses based on locus, the brain-injured groups were compared with the combined control group. Descriptions of the population and of the means of determining somatosensory status and locus of lesion are given in earlier publications (2, 3, 4, 5, 6).

Experimental Design

The experiment comprised tactile size judgments between two identical bronze cylinders (103.6 gm., 31.5 mm. in diameter), presented successively to the supinated palms, with varying interpolated intervals. These stimulus objects were hidden from view, and the duration of contact with the palm was kept constant at 1 sec. At no time was *S* informed of the identity of these objects. Three conditions of stimulation were employed: (*a*) affected hand alone, (*b*) normal hand alone, and (*c*) combination of the two bilateral conditions: i.e., comparison stimulus applied to affected hand following application of the standard to the unaffected, and the converse. In each condition *S* was required to state whether the comparison (second) stimulus object was larger or smaller than the standard (first).

The five time intervals interpolated between the standard and comparison stimuli were: 0.1, 1, 2, 3, and 5 sec. All five intervals were used in each of the three conditions, and each was repeated five times, making a total of 100 judgments for each *S* (25 for each unilateral, and 50 for the combined bilateral conditions). Approximately 8 sec. elapsed between each judgment and the onset of the standard stimulus of the next pair.

RESULTS

The principal comparisons in this experiment were: (*a*) *Condition of stimulation:* stimulation of affected hand alone, normal hand alone, and bilateral presentation of stimuli. (*b*) *Interval:* interpolation of 0.1, 1, 2, 3, or 5 sec. between standard and comparison stimuli. (*c*) *Symptom:* a brain-injured group with somatosensory impairment of the hand, a brain-injured group without such impairment, and groups with

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[1] The program of research of which this study is a part is supported by the Commonwealth Fund of New York, and by the Office of the Surgeon General (Department of the Army), Contract DA-49-007-MD-312.

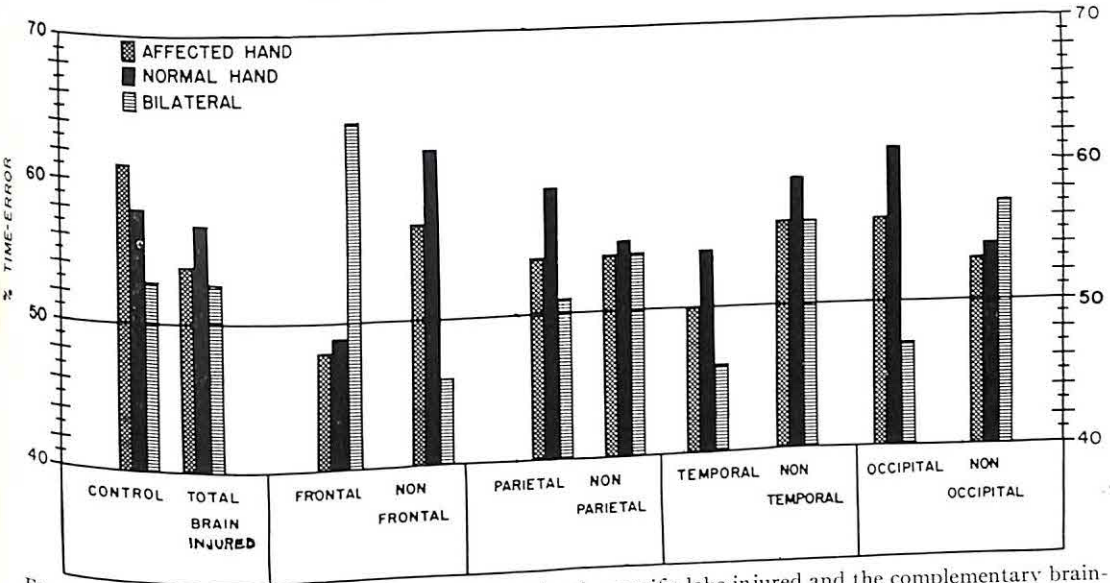

FIG. 1. Per cent mean time error. Results are shown for the specific lobe injured and the complementary brain-injured groups. Means are given for the unilateral conditions (affected hand and normal hand) and bilateral condition. All time errors greater than 50 per cent are negative, those less than 50 per cent are positive.

peripheral nerve injury of the arm or leg. (*d*) *Locus:* frontal and nonfrontal brain-injured, parietal and nonparietal brain-injured, etc.

Sign of the Time Error

The average time error for all groups was negative (Fig. 1). Only that of the brain-injured nonsensory group, and of the temporal lobe group failed to reach significance. Of the 60 *S*s, 22 overestimated the size of the second stimulus to a significant degree (negative time error), and only 2 *S*s showed a significant positive time error. This greater proportion of negative to positive time errors was significant ($p < .001$).

Conditions of Stimulation

When groups and intervals were combined, all three conditions of stimulation (unilateral as well as bilateral) produced negative time errors significantly greater than chance ($p < .001$). Bilateral stimulation produced significantly fewer negative time errors than either the affected hand alone ($p < .05$) or the normal hand alone ($p < .02$). ($F = 3.63$, $p < .05$; cf. Figs. 1 and 2.) An exception to this general finding, discussed below, was the result obtained for the frontal group.

Interval-Condition Interaction

When all groups and conditions were combined, the three longer intervals (2, 3, and 5 sec.) each produced negative time errors significantly greater than 0.1 sec. ($F = 2.97$, $p < .05$; the *t*'s resulted in p values ranging from $< .02$ to $< .001$.) These time errors were also significantly greater than chance ($p < .01$). However, comparison of conditions revealed significantly differential effects of the intervals ($F = 2.17$, $p < .05$; cf. Fig. 2). Thus, the intervals produced no differential effects on the time error for bilateral stimulation. However, for both unilateral conditions, the greater the interval, the greater the negative time error. This tendency was demonstrated by significant differences between the following intervals. On stimulation of the affected hand alone, the 5-sec. interval produced a significantly greater negative time error than 0.1, 1 sec. ($p < .001$), or 2 sec. ($p < .05$); the 3-sec. interval produced a significantly greater negative time error than 0.1 sec. ($p < .02$) or 1 sec. ($p < .01$). For the normal hand 1, 2, 3, and 5 sec. each produced greater negativity of the time error than 0.1 sec. ($p < .001$ for 1, 2, and 5 sec.; $p < .01$ for 3 sec.).

Differences among Groups

The presence or absence of somatosensory defect did not differentiate brain-injured groups from controls or from one another with regard to the magnitude of the negative time error. When the groups were divided

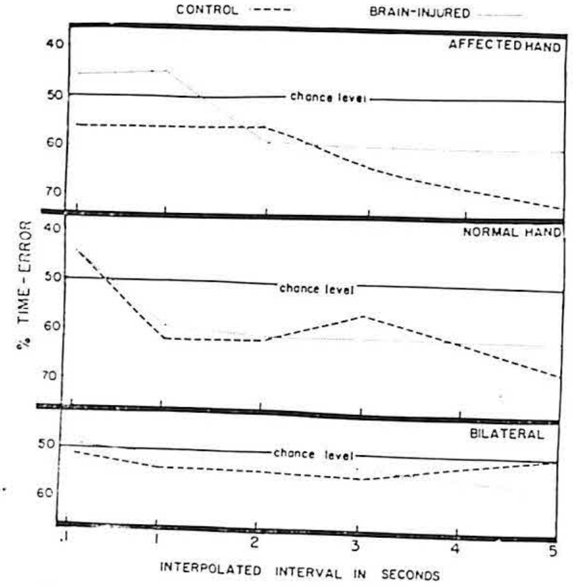

FIG. 2. Per cent time error as a function of interpolated time. The functions shown are for control and brain-injured, and for the unilateral conditions (affected hand, and normal hand) and bilateral condition. Points below the chance line (50 per cent) represent negative time errors; those above are positive.

according to the locus of the brain lesion (Fig. 2), there was a significant interaction between group and condition in one of the comparisons, i.e., the one between frontals, nonfrontals, and controls ($F = 3.95$, $p < .01$).

When either affected or normal hands were stimulated alone, time errors for both controls and nonfrontals significantly exceeded chance ($p = .051$ for affected hand of nonfrontals; for all others $p < .01$). For the bilateral condition, however, neither group had a significant time error. The frontals, however, exhibited the opposite pattern. They showed a significant time error for the bilateral condition ($p < .02$), but not for either of the unilateral conditions.

The intergroup differences were consistent with these results. Thus, whereas the frontals demonstrated a significantly greater time error in the bilateral condition than the nonfrontals ($p < .01$), they showed a significantly smaller time error than the nonfrontals for the normal hand ($p < .05$), and a significantly smaller time error than the controls for the affected hand ($p < .05$). The intragroup comparisons of the conditions likewise showed the nonfrontals to have significantly less time error for the bilateral condition than for the affected hand ($p < .05$) or the normal hand ($p < .01$); the frontals tended to show the reverse relationship ($p = .051$).

Correlations between the mean of the unilateral conditions and that of the bilateral condition yielded *r*'s of: .39, .04, and −.15 for the frontals, nonfrontals, and controls, respectively. None of these is significantly greater than chance.

DISCUSSION

It is clear from the present study that there are differences as well as similarities between the effects of brain injury on the abilities to judge size and weight.

In the present study, the sign of the time error was generally negative regardless of presence or absence of brain injury, that is, the size of the second stimulus object was consistently overestimated with regard to the first. This finding closely parallels that for tactile weight judgment (6), as well as for judgment in other modalities (1).

The finding that time error obtained on unilateral stimulation generally exceeds that obtained on bilateral stimulation is also in agreement with the earlier study on weight judgment (6). According to that study groups differentiated by somatosensory status did not differ with regard to their time error. In the present study, too, groups with and without somatosensory defect did not differ with regard to their time error.

There are also some major differences between the results of the present study and those of the study on time error for weight judgment. First, despite some similarity, none of the *r*'s between the mean time errors for size and weight judgment exceeded chance levels for the controls (.19), total brain-injured population (.34), or any other grouping of the brain-injured. Second, whereas duration of interpolated interval was not a significant variable for weight judgment, it produced significantly differential effects on the time error in the present study. Thus, aside from other possible differences in weight and size discrimination, time error for size, but not weight judgment, is dependent upon the time course of stimulation, at least for the conditions studied. Third, whereas those with parietal lobe lesion demonstrated significantly greater negative time errors for weight judgment than a group with brain injury exclusive of the parietal lobe, or a non-brain-injured control group, the time error for tactile size judgment did not significantly differentiate groups with or without lesion to the parietal lobe. In fact, for size judgment, the group with injury to the frontal lobe was significantly different from all others. This difference was reflected in a changed relationship between the unilateral and bilateral conditions of testing. For the controls and nonfrontals time error obtained on unilateral stimulation exceeded that obtained on bilateral testing; the frontals demonstrated the opposite pattern.

It is difficult to relate these findings to those of other studies on effects of brain injury in man, since similar investigations are so rare. However, the present experiment may have some bearing on certain studies of subhuman primates. There are numerous reports that monkeys with bifrontal lesion are defective on delayed response testing, the deficit increasing with duration of delay. The present study has demonstrated differential time error also as a function of duration of interpolated delay. The presence of significantly different time error patterns in groups with frontal lesion as opposed to control or nonfrontal brain-injured groups may reflect impairment of neural mechanisms in man, which are similar to those underlying delayed response in the lower primate.

SUMMARY

Time errors between the supported hands, and for each hand alone, on estimation of relative tactile size, were determined for four groups of 15 *S*s each. These groups consisted of veterans with: (*a*) traumatic brain injury and consequent somatosensory deficit of the hand, (*b*) traumatic brain injury without such somatosensory deficit, (*c*) peripheral nerve injury of the arm, (*d*) peripheral nerve injury of the leg (controls). Other divisions of the brain-injured *S*s were made on the basis of locus of lesion; i.e., frontal, and brain-injured nonfrontal groups, parietal and nonparietal, etc.

Three conditions of stimulation were employed. Stimuli were applied successively to: (*a*) normal hand alone, (*b*) affected hand alone, and (*c*) the comparison stimulus was applied to one hand following application of the standard to the other hand. Five intervals were interpolated between the standard and comparison stimuli in each condition. These were: 0.1, 1, 2, 3, and 5 sec.

Time errors were generally negative for all groups and under all conditions. However, errors obtained on unilateral stimulation of either affected or normal hand were significantly greater than those obtained on bilateral stimulation when all groups were combined. For the bilateral condition there were no significant differences in time error among any of the interpolated intervals. For stimulation of either the affected or normal hands alone, however, the greater intervals produced significantly more negative time errors than the lesser intervals.

None of the groups classified on the basis of somatosensory status produced significantly different time errors from any other group so classified. Those with lesion of the frontal lobe, however, demonstrated a significantly different pattern in their time error functions as compared with nonfrontals and controls. Controls and nonfrontals demonstrated significant negative time errors for both unilateral conditions; their time error for the bilateral condition was not significantly greater than chance. The frontals, on the contrary, had a significant negative time error for the bilateral condition, but not for either unilateral condition. This difference between groups with and without frontal lesion may reflect interference with neural processes similar to those involved in the delayed response performance of frontal monkeys.

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HOARDING AND AGGRESSIVE BEHAVIOR IN RATS

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The results of a previous investigation (4) showed significant differences between the hoarding behavior of two inbred strains of rats—a group of black-hooded rats started hoarding sooner and collected more pellets than did a comparable group of Irish rats. However, considerable individual differences were also found for the hoarding scores within each of the strains of animals employed. The present investigation is concerned with individual differences in a genetically homogenous group of rats and explores the hypothesis that hoarding is related to aggressive behavior of rats.

The factor of aggression in the hoarding situation is suggested by Weininger (5), who found that dominant rats accumulated more food pellets than did their submissive cage mates, and by Hess's findings (2) that the hoarding performance of shy rats differed from that of non-shy animals. However, these investigators did not specify the strains of animals which were used in their investigations. Genetic differences in aggressiveness were investigated by Hall (1) who concluded that "the basic determiner of fighting is a genetic one" (1, p. 311). Hoarding activity in a genetically homogenous group of *S*s may therefore be unrelated to the aggressive behavior of the animals, and the present investigation will show that these two variables are independent of each other.

METHOD

Subjects

The *S*s, 20 female and 16 male rats, were the progeny from the matings between inbred strains of black-hooded and Irish strains, respectively. Thirty-four *S*s were born to black-hooded and 2 *S*s to Irish mothers. The parent rats had been used in a previous experiment (4). The *S*s were born in 7 litters, were weaned at the age of 5 weeks, and were then raised in group cages of male and female rats, with 4 to 7 in each cage. At the start of the experiment the *S*s were between 155 and 190 days old. They were weighed at approximately weekly intervals.

Procedure

Hoarding trials. The animals were in two groups for hoarding trials. The first group consisted of 20 female and 8 male rats; the second one, 8 males. The latter group was placed in the hoarding apparatus 35 days after the first group started the experiment. Six days prior to the first hoarding trial the *S*s were put into individual cages and were placed on restricted feeding of two Purina Lab Chow pellets (approximately 15 gm.) daily. Hoarding trials were conducted in individual closed alleys which were similar to those previously described (4), except that the alleys were only 30-in. long. Each daily 20-min. hoarding trial was preceded by a 40-min. feeding period, when *S* was permitted to eat two pellets. Hoarding trials were conducted for each *S* until its daily hoarding scores showed no systematic changes for a period of 12 consecutive days. The mean number of pellets collected per trial during these 12 trials was taken as the hoarding score for each rat.

After termination of its hoarding trials each *S* was placed in a different individual cage, where it was permitted unlimited feeding until the start of the aggression experiment.

Aggression trials. Aggressiveness was determined on the basis of fights between pairs of hungry rats over food pellets. The aggression experiment began 60 days after the start of the first hoarding experiment. Four groups of *S*s were set up, each consisting of five females and four males, according to the onset of hoarding. The *S*s in group A started hoarding between trials 1 and 3, those in group B between trials 3 and 7, those in group C between trials 8 and 22, and *S*s in group D between trials 18 and 27.

Three days prior to the first aggression trial the animals were weighed and placed on deprivation feeding. During the aggression experiment *E* attempted to keep the weight of each *S* between approximately 90 and 95 per cent of its predeprivation weight. Each fight was between two *S*s of the same sex from different hoarding groups. Each *S* had one aggression trial per day for five successive days. It fought with different rats on consecutive days, and during the last three trials it was paired with *S*s from each of the other groups.

At the start of a trial the two *S*s were placed in a wire-screen enclosed wooden box with a floor 17 in. by 22 in. and a height of 10 in. After the *S*s had been in the box for at least 10 min., *E* held a food pellet between them until both *S*s had their teeth in opposite ends of the pellet. The rat which after some fighting took possession of the pellet was considered the winner of the bout and was permitted to hold it for 25 sec. If the loser of a bout pulled the pellet away from the winner, the former was considered the winner of a sec-

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[1] This investigation was supported by a grant from the Hixon Fund.

ond bout. In order to reduce stereotyped behavior patterns, as described by Seward (3), a maximum of four bouts was conducted consecutively. This was followed by an intermission of 5 to 10 min. When a rat had won three or four bouts in a row, the pellet was given to its submissive opponent, and the bout was terminated when the aggressor took possession of the pellet.

The winner of a bout was given a score of 1, the loser a score of 0. Each aggression trial consisted of ten bouts. The sum of an *S*'s scores during the last three trials was its aggression score. The Aggression Scale, therefore, had a range from 0 to 30, with a mean of 15. The mean aggression score for each of the four groups of *Ss* was computed.

RESULTS

Hoarding

The median trials of onset of hoarding for the four groups of *Ss* are shown in Table 1. No marked differences on this variable were observed between the male and female *Ss*—the median day for onset of hoarding was 8.5 for the males and 8.0 for the females. An analysis of variance for onset of hoarding of the four groups yielded an F ratio of 179 ($p < .001$), which shows that the *Ss* were placed in their respective groups in a nonrandom manner.

The magnitude of hoarding is expressed by the mean number of pellets collected per rat during the 12-trial period. The mean hoarding score for all the female *Ss* was 54.2 ($\sigma = 13.5$), and for all the male *Ss* it was 48.2 ($\sigma = 15.1$) pellets. Since the difference between these means yielded a t ratio of only 1.20 ($p > .10$), it was possible to combine the data for the male and female *Ss*. The mean hoarding scores for the four groups of *Ss* are shown in Table 1. An analysis of variance of hoarding scores for these groups yielded an F of 2.07 ($p > .05$). The rank-order correlation coefficient between onset and magnitude of hoarding for the 36 rats was .40 ($SE = .146$), which indicates a small, but significantly larger than zero, correlation between these variables.

Aggression

An *S*'s aggression score is based on the results of its last three aggression trials. In order to obtain an indication of the reliability of the method employed, aggression scores for two series of fights between the same pairs of *Ss* were correlated. Each *S* had been paired with the same opponent on the second and fifth trial. The product-moment correlation between these sets of scores for the 18 pairs was .750 ($SE = .106$). This correlation might also be an expression of dominance-submission relations which were set up during the first trials and then persisted during the second fights. If these relations had been established, one might expect a bimodal distribution of aggression scores, i.e., most *Ss* would have either low or high scores. The distribution of aggression scores was, however, unimodal and indicative of a normal curve—11 *Ss* scored between 1 and 12, 12 *Ss* scored between 13 and 17, and 13 *Ss* scored between 18 and 26. It may therefore be concluded that the method for conducting and scoring aggression trials was reasonably reliable.

The mean aggression scores for the four groups of *Ss* (Table 1) show no marked or systematic differences among the groups. An analysis of variance of these scores yielded an F of 1.78 ($p > .05$). The rank-order correlation coefficient between onset of hoarding and aggression for the 36 rats was .033 ($SE = .176$), and the corresponding coefficient between amount of hoarding and aggression was .067 ($SE = .160$).

Since fighting ability may depend on both the rat's weight and its weight loss during deprivation, *E* attempted to control these variables during the experiment. At the start of the aggression experiment the mean weights for the four male groups were between 190 gm. (group A) and 263 gm. (group C), and for the females they were between 182 gm. (group A) and 202 gm. (group B). There were also no substantial differences among the mean weight losses of the groups, which were between 8 per cent and 10 per cent of the groups' predeprivation weights.

TABLE 1

Mean Hoarding and Aggression Scores of Four Groups of Rats

Group	Hoarding		Aggression Score (Mean)
	Onset (Median Day)	Mean Number Pellets/Trial	
A	2	60.5	17.8
B	5	52.5	11.2
C	15	44.6	15.3
D	24	48.9	15.7

DISCUSSION

The *S*s used in the present investigation were the hybrid from two pure strains of rats. The *S*s may therefore be considered genetically identical, except for sex differences. The genetic factor in hoarding is supported by the findings that the male and female groups did not differ significantly in their hoarding performance, and that the mean hoarding score for the total group of *S*s was approximately equal to that of the high-hoarding parent strain and was significantly higher than the hoarding score for the low-hoarding parent group (4). However, the scores of onset of hoarding for the present *S*s did not appear to be related to those obtained for either of the parent strains.

In the present investigation several experimental variables were held constant, such as genetic background, weaning time, the upbringing of the *S*s prior to hoarding tests, the period of isolation of individual *S*s, the degree of deprivation, and the experimental arrangement. The possibility was also considered that individual differences in hoarding and aggressive behavior were related to differences between litters. The *S*s from two litters showed a tendency to be late hoarders; ten of these rats were in groups C or D, whereas only three of their littermates were early hoarders (groups A or B). However, there were approximately equal proportions of early and late hoarders among each of the five other litters. Moreover, an analysis of the aggression scores did not reveal any relationships between aggressiveness and litter origin.

On the basis of the present investigation, it may be concluded that, in a group of genetically homogenous rats, there are considerable individual differences in both the onset and magnitude of hoarding, but the variables of hoarding and aggressive behavior are not related.

SUMMARY

The *S*s, 20 female and 16 male rats, were the progeny from the matings between two inbred strains, which had previously been found to be high hoarders and low hoarders, respectively. The *S*s' hoarding performance and aggressiveness were determined in independent experiments. Aggression scores were based on the outcomes of fights between pairs of rats. The amount of pellet collection during the hoarding trials was approximately equal to that of the *S*s' high-hoarding parents. Scores for onset of hoarding, however, were not related to those of either parent group. The correlation between onset of hoarding and aggression was .033, and the correlation between amount of hoarding and aggression was .067.

It was concluded that, in this group of genetically homogenous rats, there were considerable individual differences in scores for both the onset and magnitude of hoarding, but these were not related to the aggressive behavior of the *S*s.

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THE INFLUENCE OF SEX HORMONES ON SOCIAL BEHAVIOR IN MONKEYS[1]

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Studies conducted on such widely different infraprimate animals as fish (12), reptiles (13), birds (1), and mammals (2) have shown that androgens generally enhance the dominance of both male and female animals, while estrogens either reduce aggressiveness or are without effect. The few investigations of the behavioral effects of gonadal hormones in primates have been confined to the chimpanzee. Yerkes (16), Nowlis (14), and Crawford (9), who studied male-female and female-female pairs in a competitive feeding situation, reported that subordinate females often obtained more food while in estrus than at other times. Birch and Clark (5, 6, 7, 8), working chiefly with castrate chimpanzees, reported the effects of administering sex hormones to one or another member of like-sexed pairs. After androgen treatment, a subordinate female obtained most or all the peanuts in a competitive feeding situation; prior to this treatment she had obtained few, if any, of the nuts. Estrogen had the same effect on this female. After androgen treatment, a dominant male whose peanut-getting priority was not complete, obtained nearly all the nuts; estrogen had the effect of making him subordinate to his cage mate. Nowlis (14) reported estrous enhancement of the food scores of females in eight of the ten like-sexed and different-sexed pairs he studied.

Other studies suggest that these effects do not invariably occur in chimpanzees. In Yerkes' (16) study describing the relationship between priority of response and the sexual status of the female, more than half the male-female combinations (23 of 45) were discarded because the "typical" effect (i.e., the male dominates the feeding situation except when the female is in estrus) was not obtained. Crawford (9) found a reliable increase in food scores of subordinate members of female pairs during their maximum estrus phase in only 6 of the 16 pairs he studied.

Since it is questionable whether the phenomena described by Birch and Clark may be generalized to include all chimpanzees, it is also questionable whether they apply to all primates. The present study was designed to investigate the effects of gonadal hormones on dominance behavior in another primate, the rhesus macaque (*Macaca mulatta*).

METHOD

In Part 1 of this experiment two groups of five animals were studied; in Part 2, four groups of two.

Part 1

Subjects

Two groups of young macaques were used; one consisted of five females, Miriam, Esther, Naomi, Ruth, Olga; the other, of five males, Al, Les, Hal, Frank, Gene. All animals had been gonadectomized at least two months prior to the experiment. The animals in each group were housed either together in a large group cage of dimensions 8 ft. by 4½ ft. by 7 ft., or separately in individual cages of dimensions 2 ft. by 2½ ft. by 2½ ft. The periods of group- and individual-cage living are reported in Table 1.

Procedure

Testing. When housed in the group cages, each group was observed daily at a regular time. The *E* sat in front of the group cage and introduced 75 peanuts, one at a time, through the wire mesh of the cage front by means of a feeding device which consisted of a length of 1½-in. pipe mounted obliquely on a stand so as to extend 1 ft. into the large cage. The *E* recorded which animal got each peanut and the dominant-subordinate interaction that occurred. At the end of the observation session, Rockland monkey pellets were thrown into the cage in amounts sufficient to make up the daily total ration of 80 cal/kg body weight per animal (exclusive of peanuts). This diet was supplemented three times a week with one-half orange per animal. The animals were fed the same diet when housed individually.

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Establishing the hierarchy. The characteristic "straight-line" hierarchy found in groups of macaque monkeys has been frequently described (11). In this social arrangement, the direction of all aggressive or dominant interaction is invariant, and always unidirectional. Thus, if X engages in dominant interaction against Y, he is said to be dominant over Y. Once the hierarchy is established (and this usually takes place very rapidly), Y never engages in dominant interaction against X. If Y is in turn dominant over Z in the group, then X will also invariably be dominant over Z. This kind of group relationship will be summarized by the notation X→ Y→ Z.

In terms of one of the five-animal groups used in this study, i.e., Al, Les, Hal, Frank, Gene, the hierarchy was considered established once the four bits of dominant interaction Al→ Les, Les→ Hal, Hal→ Frank, and Frank→ Gene were observed. After these four acts were observed, it could have been confidently predicted that all dominant interaction between Al and Hal would have the direction Al→ Hal, all dominant interaction between Les and Gene, the direction Les→ Gene, etc. These four acts occurred on the first day of observation. This nonquantitative unidirectional nature of dominant interaction in the group defines the term hierarchy as it is used in this study.

Recording of behavior. Three categories of behavior were recorded during the daily session: dominant acts, peanut-getting acts, and subordinate acts. A dominant act was recorded for an animal engaging in one of the following kinds of behavior:

1. Mild attack. The animal (A) assigned the dominant act chases, pushes, strikes or pulls the tail or hair of another animal (B).

2. Severe attack. A bites B.

3. Displace. A displaces B from a position the latter was occupying.

4. Other moves. As A approaches or turns around, B moves away although no aggressive intent is discernible on the part of A toward B.

5. Other fails to initiate action toward peanut. Although a peanut has fallen farther from A than B, B makes no attempt to reach for the peanut for at least 5 sec. During this time, B watches A's movements closely.

6. Threatening gesture. A growls, glowers threateningly, adopts an "all fours" stance, wags his head aggressively in the direction of B, or crouches as if to spring after B (but does not actually attack B). One, or several of these behaviors in combination, constitutes a threatening gesture.

7. Sniffs mouth. A smells at the mouth of B. This action, like that described in number 8, was often followed by an attempt to steal food.

8. Passive manipulation. A lifts one of B's limbs or opens B's mouth, while B passively submits to A's handling.

9. Head stand. A stands on B's head, shoulders, or back as A gets a nut or prepares to catch one.

10. Mounts feeding pipe. A sits on or supports his weight by the feeding pipe, using his front paws, for at least 5 sec. A is thus in a position to catch the peanuts as they fall from the pipe.

TABLE 1

Experimental Plan of Part 1

Period	Length (days)	Description
1	10	Group cage base line measures
2	2	Control separation
3	10	Group cage postcontrol separation measures
4	2	Separation to implant no. 5 animal with androgen
5	25	Group cage measures of hormone effect
6	2	Separation to remove pellet from no. 5 animal
7	25	Group cage posthormone measures
8	2	Separation to implant no. 2 animal with androgen
9	25	Group cage measures of hormone effect
10	2	Separation to remove pellet from no. 2 animal, and to implant no. 5 animal with estrogen
11	25	Group cage measures of hormone effect
12	2	Separation to remove pellet from no. 5 animal
13	15	Group cage posthormone measures
14	2	Separation to implant no. 2 animal with estrogen
15	25	Group cage measures of hormone effect
16	2	Separation to remove pellet from no. 2 animal
17	25 (females) 15 (males)	Group cage posthormone measures

11. Steals peanut. A takes a nut from B's paw or from the ground where B had placed it.

12. Attempts to steal peanut. A tries to take a nut from B but does not succeed.

A peanut-getting act was recorded for an animal engaging in one of the following kinds of behavior:

1. Gets peanut. A gets a peanut without competition from any other animal, or before another animal gets close to the nut.

2. Attempts peanut—successful. A and B contest or try actively for a nut and A gets the nut.

3. Attempts peanut—unsuccessful (see 2). B is credited for his attempt.

A subordinate act was recorded for an animal engaging in one of the following kinds of behavior:

1. Cringe or short withdrawal. B grimaces coweringly, or runs from A a distance less than the length of the cage, without changing his plane of motion (i.e., does not move from the floor to the wall or vice versa).

2. Long withdrawal. B changes his plane of motion or jumps from one side of the cage to another.
3. Flight. B runs or leaps rapidly away from A, placing as much distance as is physically possible between himself and A.
4. Stops action toward peanut. See B's role in dominant act 5.
5. Has mouth sniffed. See B's role in dominant act 7.
6. Passively permits manipulation. See B's role in dominant act 8.
7. Is stood upon. See B's role in dominant act 9.

Dominant acts 1 to 9 are interanimal dominant acts for which both a dominant and a subordinate act were scored; dominant acts 10 to 12 are single-animal dominant acts for which only a dominant act was scored.

Although not used in dominance scoring, all instances of mounting, grooming, and presenting were recorded.

Each animal received a tally of 1 for each dominant, subordinate, and peanut act in which he engaged. The daily total peanut acts for an animal, not including unsuccessful attempts, constituted his *Peanut Score* (P Score). The daily total of all dominant acts and unsuccessful peanut attempts constituted his *Other Dominance Score* (O Score). The sum of these two scores made up his *Total Dominance Score* (D Score), and the sum of all subordinate acts made up an animal's *Subordination Score* (S Score).

In the groups studied, all but the least dominant animal (no. 5 in the hierarchy) engaged in interanimal dominant acts, single-animal dominant acts, and in peanut-getting acts. Animal no. 5 was never observed to initiate interanimal dominant acts. All animals except the number 1 animal in the hierarchy of each group engaged in subordinate acts. Changes in P, O, D, and S Scores and/or changes in the hierarchy were taken to be evidence of an effect of the hormone on dominance behavior.

Reliability. In order to determine the interrater reliability of this system of recording behavior, two observers trained in this method made separate tallies of the behavior occurring during three observation sessions of the male colony. The two observers agreed as to the hierarchy-ranks of the five animals (i.e., Al→ Les→ Hal→ Frank→ Gene). In no instance did one observer score as dominant an act that the other observer scored as subordinate. Ten per cent of the dominant and subordinate acts on the scoring sheets of the two observers were scored as not seen by both observers. Of the remaining acts, there was 95 per cent agreement on the scoring. Of the peanut acts (including unsuccessful attempts), 99.6 per cent were seen by both observers, and they agreed on the scoring of 98.3 per cent. The three-day D-Score and S-Score totals of the five animals according to Observer 1 correlated .99 with the corresponding totals of Observer 2.

Validity. In order to determine the validity of this system of recording behavior, the rank of the animals in each group according to their position in the hierarchy was compared with their rank according to mean D Score and S Score during the first two control periods of the experiment (per. 1 and 3, Table 1). The hierarchy of the female colony, ranked from most to least dominant, was Miriam, Esther, Naomi, Ruth, Olga; in order of mean D Score, from highest to lowest, the animals ranked Miriam, Esther, Ruth, Naomi, Olga. The rho correlation between the two sets of ranks was .90, $p < .05$. The hierarchy-ranks of the male colony were identical with the mean D-Score ranks: (from most to least dominant) Al, Les, Hal, Frank, Gene (rho = 1.00). In contrast with the high correlations between hierarchy ranks and D-Score ranks, the correlations between hierarchy ranks and S-Score ranks were low and not significant. Ranked by S Scores, from highest to lowest, the females were: Esther, Ruth, Naomi, Olga, Miriam; the males were: Les, Frank, Hal, Gene, Al. The rho correlation of these rankings with hierarchy-ranks (from most to least dominant) was −.10, $p > .05$ in each case.

The D and S Scores provide a more sensitive measure of the group structure and interaction than just the hierarchy-ranks. It is for this reason that changes in P, O, D, and S Scores, as well as changes in hierarchy-rank, were used to evaluate the effects of the hormones. In addition, changes in score-rank were taken to be evidence of an effect of the hormone on dominance behavior.

Hormone administration. Pure crystalline pellets of hormone were implanted by aseptic technique in the back of the anesthetized animal. A small incision was made in the infrascapular portion of the back, the pellet placed on top of the fascia several inches away from the site of the incision, and the wound closed with interrupted sutures. The estrogen pellets consisted of 25 mg. of Progynon (estradiol); the androgen pellets were 75 mg. of Oreton-F (testosterone propionate).[3] All pellets were removed 28 days after implantation. In addition, the tissue surrounding the pellet was excised to insure removal of all the hormone.

Pellet implantation was used in preference to frequent injection of hormone because it necessitated only one breaking-up of the colony. Moreover, this method of administration has been described as tending to simulate natural secretion of the hormone and as providing regular absorption rates (15).

Design

Base line measures of the group structure and interaction were obtained. Then, the animal lowest in the hierarchy (i.e., no. 5) was treated with androgen. After suitable measures had been obtained, the pellet was removed and posthormone measures obtained. Next, the number 2 animal in the hierarchy was treated with androgen. This treatment sequence was then repeated with estrogen. The plan of the experiment is presented in Table 1. The procedure was identical for the two colonies except that period 17 was 25 days for the female colony as compared with 15 days for the male colony.

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[3] The hormones used in this study were supplied by the Schering Corporation of Bloomfield, New Jersey.

TABLE 2
Experimental Plan of Part 2

Period	Length (days)	Description
1	10	Pair cage base line measures
2	2	Control separation
3	10	Pair cage postcontrol separation measures
4	2	Separation to implant subordinate animals with hormone (Viola and Ike with androgen, Ruth and Abie with estrogen)
5	25*	Pair cage measures of hormone effect

* 20 days in the case of Sally and Ruth.

Part 2

In Part 2, groups of two instead of five monkeys were studied. The observation procedure, method of recording behavior, and means of administering hormones were identical with those described in Part 1.

Subjects

Eight young gonadectomized monkeys, four of each sex, were divided into four like-sexed pairs. The pair members were as follows: Teddy and Ike, Jake and Abie, Naomi and Viola, Ruth and Sally. Although Ruth and Naomi had been used in Part 1 of this study, neither had been subjected previously to hormone administration. The members of each pair were housed either together in a large cage of dimensions $3\frac{3}{4}$ ft. by $4\frac{1}{2}$ ft. by $6\frac{1}{2}$ ft., or separately in individual cages of dimensions 2 ft. by $2\frac{1}{2}$ ft. by $2\frac{1}{2}$ ft.

Design

The procedure was identical for all pairs: after obtaining base line measures, the subordinate member of each pair was treated with hormone. One subordinate male received androgen, the other subordinate male, estrogen. Similarly, one subordinate female received estrogen, the other subordinate female, androgen. The experimental plan is summarized in Table 2. Since no hierarchy-rank or score-rank was changed by hormone treatment, no posthormone measures have been included.

RESULTS

Physiological Effects of Hormones

Implantation of estrogen invariably produced marked swelling and reddening of the sex skin in the females and the scrotal sac in the males. In addition, both sexes displayed swollen nipples and faces, as well as pronounced wrinkling and folding of the skin on the back and legs. These changes are the typical result of estrogen treatment of macaques (18). The swelling and reddening usually disappeared within ten to fifteen days after removal of the estrogen; the wrinkling and folding occasionally persisted in mild form for a somewhat longer time.

Except for one male (Ike), which showed slight reddening of the skin around the penis, and one female (Viola), whose sex skin reddened slightly, no animal showed external physical effects of androgen.

Behavioral Effects of Hormones

Part 1

Dominance and subordination. In no case was any hormone treatment accompanied by a change in the dominance-subordination relationship existing between two animals prior to such treatment. There were no observed instances of dominant interaction contrary to the direction implicit in the straight-line hierarchies of the two colonies, which persisted as originally established throughout the duration of the study. The hierarchy of the male colony was Al → Les → Hal → Frank → Gene; the hierarchy of the female colony was Miriam → Esther → Naomi → Ruth → Olga. The other behavioral results are illustrated in Figures 1 and 2. These figures illustrate the means of the various scores (P, O, D, and S) for the two colonies in each of the experimental periods. The ranking of the animals according to each of these scores in any experimental period can be determined by noting the ordinate values of the scores at that period, i.e., the animal with the highest mean score in any period ranks highest, and the animal with the lowest mean score ranks lowest. The ranking of the animals of each colony according to the hierarchy was usually consistent with the ranking according to P Scores, O Scores, and D Scores (Fig. 1 and 2). The animals that ranked first in the hierarchy (Al and Miriam) usually ranked first on these measures; the animals that ranked second in the hierarchy (Les and Esther) usually ranked second on these measures. The scores of the three remaining animals in each group were usually rather close, and there was more variation among their score-ranks than in the ranks of the animals first and second in the hierarchy. With regard to S Scores (Fig. 1 and 2) Les and Esther (the animals second in the hierarchy) usually

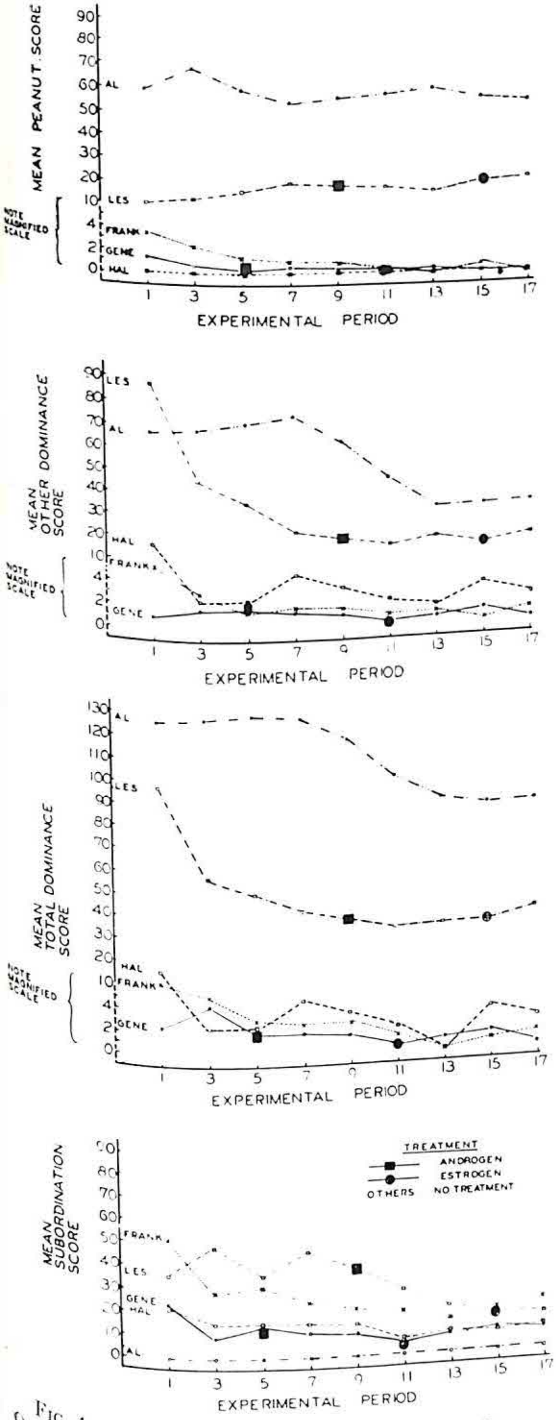

FIG. 1. Reading from top to bottom, Peanut Scores, Other Dominance Scores, Total Dominance Scores, and Subordination Scores, 5-male colony.

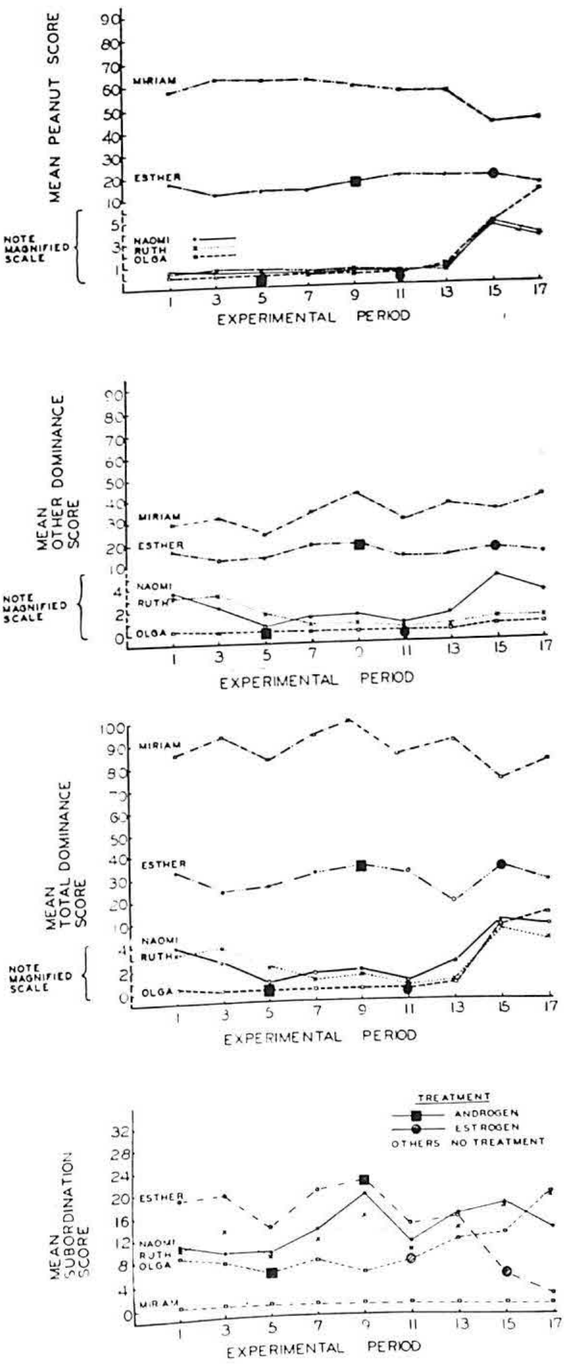

FIG. 2. Reading from top to bottom, Peanut Scores, Other Dominance Scores, Total Dominance Scores, and Subordination Scores, 5-female colony.

ranked highest, whereas Al and Miriam (first in the hierarchy) with zero scores invariably ranked lowest.

It is apparent from these figures that there was only one change in score-rank of more than one position associated with hormone treatment. Esther's S Score (Fig. 2) fell from rank 2 in the pre-estrogen period (per. 13) to rank 4 in the estrogen period (per. 15). Although the change in S Score was significant ($p < .01$), neither the absolute score value nor the score-rank reverted to the pre-estrogen level after the withdrawal of the hormone. A return to the pre-hormone level would be expected in view of Birch and Clark's (5, 6) results with estrogen treatment of chimpanzees. Significance levels were computed by means of Fisher's t test, using a pooled estimate of day-to-day variance.

There were only four other scores out of the total of 32 (8 treatments × 4 scores) that changed significantly with hormones. One of these score changes, Les' S Score, although decreasing significantly ($p < .02$) during androgen, does not appear to be attributable to the effects of the hormone. Although his S Score fell one rank at this time, there was a more significant score decrease ($p < .01$) from the androgen period (per. 9, Fig. 1) to the post-androgen period (period 11); moreover, both decreases appear to be a reflection of a gradual reduction in Les' S Score extending from period 3 to period 17. Les' O Score and D Score (Fig. 1) also decreased steadily during the experiment.

Two of the changes accompanied Gene's treatment with androgen in period 5. Gene's (and Olga's) score changes in period 5 were evaluated against the combined control data from periods 1 and 3. There were significant decreases in Gene's P Score ($p < .01$, Fig. 1) and D Score ($p < .05$, Fig. 1). The D-Score change was accompanied by a fall in rank of one position, and was not reversed following the withdrawal of hormone. The remaining change was a reduction in Gene's S Score during estrogen treatment ($p < .02$, Fig. 1). The S-Score change was not accompanied by a change in rank, nor did the score increase significantly after the hormone was withdrawn.

Mounting, grooming, and presenting. The only significant change in the frequency of mounting, grooming, and presenting accompanied the estrogen treatment of Esther. Her daily mean of all such acts combined increased from 0.33 in the pre-estrogen period to 3.56 during estrogen treatment ($p < .01$).

Part 2

Dominance and subordination. The data from the four pairs studied, i.e., Teddy and Ike, Jake and Abie, Naomi and Viola, and Sally and Ruth, are summarized in Figure 3. As can be seen from this figure, the priority of peanut-getting established by the dominant member of the pair in period 1 was not changed by any hormone treatment. Moreover, the direction of dominant-subordinate interaction was always Teddy → Ike, Jake → Abie, Naomi → Viola, Sally → Ruth throughout the study.

Although there were seven significant score changes in Part 2, none of them was large; the dominant animal of the pair invariably achieved a higher P, O, and D Score than the subordinate animal. The only significant change accompanying hormone treatment in the two females was a decrease in Ruth's S Score ($p < .05$). With the males, on the other hand, there were significant reductions in Abie's P Score ($p < .05$) and D Score ($p < .01$), and in Ike's P, O, D and S Scores ($p < .01$ in each case). These comparisons are based on the combined data of control periods 1 and 3 versus period 5. The highly significant reduction in all Ike's scores results from a change in the technique of peanut-getting employed by his dominant pair-mate Teddy, rather than from any hormonal effect on Ike. During periods 1 and 3, Teddy typically remained on the floor of the cage and chased each peanut as it fell from the feeding pipe. Although Teddy was clearly dominant in peanut-getting (mean P Score = 60.75), Ike managed to garner about 20 per cent of the nuts (mean P Score = 14.25), usually being attacked in connection with every peanut he got (mean S Score = 16.6). During period 5, however, Teddy adopted the technique of sitting on the pipe and catching the nuts as they fell. This had the effect not only of increasing his mean P Score to 69.56, and increasing the number of his mountings of the feeding pipe from a mean of 0.7 during periods 1 and 3 to a mean of 13.9 during period 5, it also decreased the interaction between the two animals. Thus, Ike's reduced P Score reflects Teddy's increase, Ike's lowered O Score reflects the fewer opportunities he had to attempt to get peanuts so long as Teddy sat on the pipe, and Ike's lowered D Score reflects the decrease in P and O. The decrease in Ike's S Score to a mean of 3.20 results not

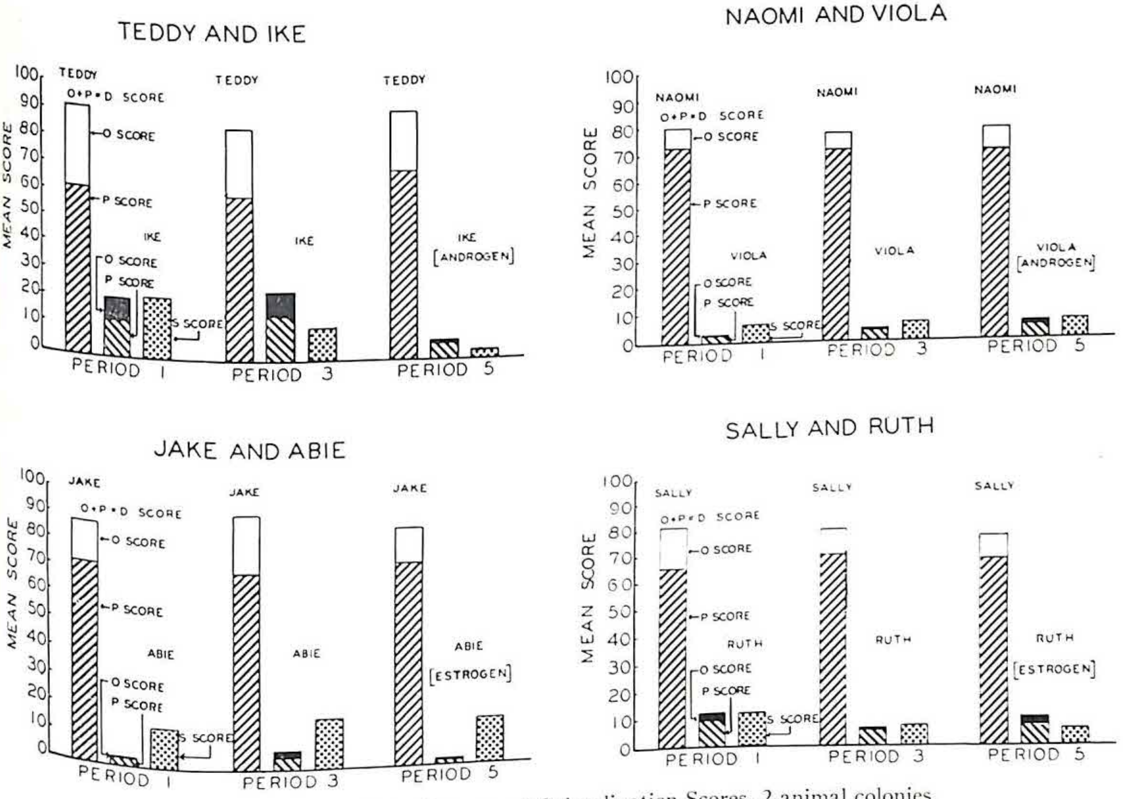

FIG. 3. Summary of Dominance and Subordination Scores, 2-animal colonies.

only from the increase in physical distance between the two animals during the sessions, but also from the fewer occasions (fewer peanuts and peanut attempts) on which Ike could provoke attacks from Teddy.

Mounting, grooming, and presenting. Mounting, grooming, and presenting were rarely seen in these pairs during the observation sessions, and there was no significant difference accompanying the treatment of any animal.

DISCUSSION

The results of this study emphasize how ineffective hormones may be in inducing changes in the social behavior of macaques. The straight-line hierarchies in the six groups that were studied remained unchanged during the course of the study. Moreover, no hormone treatment was accompanied by a score increase; the seven significant score decreases in Parts 1 and 2 that are not explainable in terms of nonhormonal factors reveal little or no consistent pattern. Two changes accompanied androgen treatment of a low-status male (Gene's P and D scores); three other changes accompanied estrogen treatment of a low-status male (Abie's P and D scores, Gene's S score); one change accompanied estrogen treatment of a high-status female in the group of five (Esther's S Score); the remaining change accompanied estrogen treatment of the subordinate member of a pair of females (Ruth's S Score). These changes are not related to changes in the frequency of observed mounting, grooming, and presenting behavior, for only one animal (Esther) showed a significant change in such behavior. Since these changes show little or no consistency and since the hierarchies remained intact, the most reasonable interpretation of the results is that gonadal hormones have no effect on dominance in unisexed macaque social groups; the changes observed in dominance and subordination scores are the result of other factors in the relationships of the animals. One of those other factors is apparently identified in the case of Ike's changes with androgen, and another is illustrated in Figure 1 in the case of Les's change with androgen.

These results are in striking contrast with those of Birch and Clark (5, 6, 7, 8). The difference does not appear to lie in differences in experimental design: both studies used castrate animals (this is true for three of the four Birch and Clark investigations) and both studies employed daily observation of the animals in a competitive feeding situation. It is not likely that the difference in age between Birch and Clark's mature chimpanzees and the young animals of the present study accounts for the difference in results. In his survey of the interrelationships between endocrine secretions and patterns of overt response, Beach concluded:

> Neuromuscular elements responsible for such hormonally conditioned behavior patterns as courtship, mating and care of the young are fully organized and ready to function relatively early in life, well in advance of the time that they will normally be activated . . . their organization is complete prior to the time that the hormones which will sensitize them to stimulation are secreted in sufficient quantities to become effective (3, p. 211).

If dominance behavior in the macaque is a "hormonally conditioned behavior pattern," it probably would have been manifested in the animals of the present study. Although these results differ markedly from those of Birch and Clark, they differ less from the results of Yerkes (16), who found no estrous enhancement of dominance in at least half the male-female combinations he studied, and the results of Crawford (9), who found no such effect in 10 of the 16 pairs he studied.

A difference between the species which may account for the difference in results relates to the character of the social relationships generally observed in the macaque and the chimpanzee. Yerkes and Yerkes (17) and Maslow (10) have noted that dominance in the chimpanzee is usually expressed in a relatively nonviolent and noncontactual manner, especially when compared with the expression of dominance in certain catarrhine monkeys, such as the macaque. One chimpanzee may dominate another completely without any observed instances of attacking or biting. This kind of social relationship has been described by Maslow as "friendly" and "protective." In the macaque, on the other hand, aggressive chasing and biting is apparently an invariable concomitant of social dominance, prompting Maslow to describe it as "brutal" and "sadistic." Yerkes' (16) and Crawford's (9) data suggest that temperamental differences may be the cause of the frequent obscuring of estrous enhancement of dominance in the female chimpanzee. Some of the reasons offered by Yerkes for atypical cases (i.e., male-female pairs in which the female dominated the feeding situation only while she was in estrus) included "unassertiveness," "timidity," and "exceptional aggressiveness or dominance" of the female. Crawford concluded, "a variety of reactive patterns built up during the life of the animal . . . may determine the outcome of any test of dominance" (9, p. 508).

Since temperamental differences may obscure hormonal effects in the relatively unaggressive chimpanzee, individual differences in aggressiveness may always act to obscure hormonal effects on dominance in unisexed macaque groups because of the greater role of aggression in the social behavior of the macaque. Hormonally induced dominance would therefore appear to be relatively weaker than the dominance resulting from other factors if the latter is pronounced among members of a species. Thus, the hormonal effects on dominance in the chimpanzee in a competitive feeding situation as described by Birch and Clark may not be demonstrated when individual members of a species are capable of wide variations in aggressiveness.

This research has emphasized that aggression and dominance are not invariably influenced by sex hormones; the social behavior of the macaque in a competitive feeding situation is markedly refractory to such treatment. Beach (4) has urged the necessity for studying many kinds of animals to avoid the error of overgeneralizing from a few; the results of the present study reiterate his point. Despite the fact that the response of several species to gonadal hormones has been investigated, it would seem to be impossible to describe the response of any other species without actually conducting the research.

SUMMARY

1. Unisexed social groups of male and female castrate *Macaca mulatta* were observed daily in a competitive feeding situation, and instances of dominant, subordinate, and other interanimal behavior were recorded.

2. After control measures of the group hierarchy and behavior had been obtained,

various members of the groups were implanted with pellets of androgen or estrogen.

3. In no case was hormone administration accompanied by changes in the hierarchy or by an increase in the number of instances of dominant behavior.

4. Although 7 of the 12 treatments were accompanied by a significant decrease in either dominant or subordinate behavior scores, the change in 2 cases could not reasonably be attributed to hormone administration, and the changes in the other 5 show little or no consistency. This suggested that gonadal hormones were without effect on unisexed groups of castrate macaques, and that the observed changes resulted from other factors.

5. It is suggested that the difference between these results and those derived from the chimpanzee is related to the greater degree of aggressiveness characterizing the social behavior of the macaque as compared with the chimpanzee.

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ACTIVITY, MANIPULATION DRIVE, AND STRENGTH IN MONKEYS SUBJECTED TO LOW-LEVEL IRRADIATION[1]

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The aim of the present project was to determine the effects of whole-body irradiation on the performance of monkeys in tests of lightly motivated behavior. General bodily activity (locomotor, postural, and membranal) was considered to be lightly motivated, as was manipulatory activity of the type described by Harlow, Harlow, and Meyer (6). Since "weakness" is a recognized feature of human irradiation sickness, a weight-pulling task with a strong (banana) incentive was included at the highest radiation level.

The basic assumption underlying the present experimental approach was that rather simple "nonmotivated" or lightly motivated behavior would better reflect the effects of minimal stresses than would difficult, complex tasks employing strong homeostatic drives. Further, in extrapolating from laboratory experiments to human behavior, it may be desirable to predict the performance of man under conditions of low motivation, which manifestly cannot be done from experiments which employ strong motivations. The hypothesis would apply equally to such external stresses as altitude, cold, and toxic gases, and to internal stresses such as fatigue, sleeplessness, and drugs. In respect to radiation, this thesis receives some support from the unpublished work of Davis,[2] who obtained a deficit in only one of a number of problems involving an edible reward. Further support is seen in the experiments of Kaplan and his associates (9, 10, 11, 15) which indicate that solution of the discrimination type of problem by monkeys under high motivation is not impaired by sublethal radiation doses and probably not by lethal doses as long as the subject is both able and willing to perform.

Since it was of interest to establish dosage threshold values for behavior abnormality as well as to quantify the relationship between dosage and behavior changes, a number of experiments were conducted using doses well below $LD_{50/30}$, which may be about 600 r. in the rhesus macaque.

METHOD

Subjects

A total of 18 young rhesus monkeys, weighing between 4 and 8 lb. at the time of irradiation, were used in four experiments. All were adapted to the laboratory procedures over a period of at least two months prior to X-ray exposure. Two *S*s irradiated with 300 r. had suffered ablation of frontal cortical areas, but excepting an unusually high level of locomotor activity, they appeared to be quite normal in all tests.

Staggering the time of exposure permitted the use of some *S*s as controls for one or more weeks before they were irradiated and joined the experimental group. For example, in the last experiment, in which the dose was 400 r., two monkeys were irradiated one week, one monkey the next week, and two more the following week. Since four monkeys were never exposed, the controls numbered seven until the second postirradiation week for the first group, when the controls were reduced to six. In the third week and thereafter, there were four controls. In Table 1 the size of control and experimental subgroups at each radiation level is shown. A decrease in the number of controls for one subgroup denotes the enlistment of the subtracted *S*s as irradiated experimentals in the following subgroup.

The two monkeys that had received 200 r. were allowed about four months for recovery and then were re-irradiated, one with 50 r. and the other with 100 r. A short time before this and about six to eight weeks after their initial exposure, two experimentals from the 300 r. group had been re-irradiated with 50 r. and two others with 100 r. Because of the relative impotency of these low doses and the small number of cases, the animals receiving 50 r. and 100 r. have been placed in one main group, as seen in Table 1.

Procedure

Strain-gauge recording of general activity. Measurement of activity began between 5:00 and 6:00 P.M. and lasted 3 hr. in the 200 r. experiment, and about 2 hr

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[2] R. T. Davis. Performance and histopathology of macaque monkeys as a function of near lethal radiation. Progress Report on U.S.P.H. Grant M-530, 1952–1953.

TABLE 1

Number of *S*s in Radiation Groups and Subgroups

Radiation Dose	No. of Experi-mentals	No. of Controls Weeks						
		−1	+1	+2	+3	+4	+5	+6
200 r.								
Subgroup I	1	2	2	2	2	2	1	
Subgroup II	1	1	1	1	1	1	1	
300 r.								
Subgroup I	2	4	4	2	2	2	2	2
Subgroup II	2	2	2	2	2	2	2	2
Subgroup III	2	0	0	0	0	0	0	0
400 r.								
Subgroup I	2	7	7	6	4	4	4	4
Subgroup II	1	6	6	4	4	4	4	4
Subgroup III	2	4	4	4	4	4	4	4
50 r., 100 r.								
Subgroup I	4	2	2	2	2			
Subgroup II	2	0	0	0	0			

in the other experiments. At the 300-r. level additional records were secured for 30-min. periods every hour from 5:00 A.M. to 10:00 A.M. A flexible brass rod bearing strain-gauges was placed in contact with one end of the home cage floor, which was suspended on springs at 400 r. (Fig. 1) or mounted on rubber at the other dose levels. In the 200 r. experiment a long narrow cage attached to the home cage was used for activity measurement. Movements were recorded with a Brush pen-motor plus a suitable inexpensive amplifier or with an Offner dynograph. Since the apparatus could handle only a limited number of simultaneous recordings (never more than six), the records are incomplete for some animals, especially at 400 r.

Observational rating of activity. An inventory of behavior, containing about 25 categories (developed by RWL), was used in the 400 r. experiment. Each monkey was rated for any display of the selected behaviors during one-min. periods for ten consecutive minutes. The *E* sat quietly in a chair near the monkey's cage and tried to avoid exciting *S* while the ratings were made. In this manner two to four observational sessions were conducted each week between 8:00 P.M. and 10:00 P.M.

Mechanical puzzles. In Figure 2 is seen the three-step mechanical puzzle which consisted of a hasp locked by a hook which was itself locked by a pin on the end of a chain. The parts were mounted on a wood panel which was fastened to the interior wall of a cage during the test period. The tester made rounds of the cages resetting any open parts every 2.5 min. for 1 hr. in the 200 r. experiment, and every 5 min. for 30 min. in the other experiments. If no part was opened, the *E* would reach in and touch the puzzle. Preirradiation testing lasted in no case less than two months, and three or more tests were run each week.

Pedometer manipulation. Eight days before the irradiation of subgroup III of the 400 r. group, the two experimental *S*s and two controls were supplied with a pedometer sandwiched between two pieces of plastic and centered inside a small wood frame (see Fig. 2). This toy was simply left on the cage floor, and readings were taken at intervals of 24 hr. A slight jiggle of the vertical pedometer or a semicomplete turnover, however gentle, would register 1 "yard" on the main scale, which was marked off in tens of yards. On a subordinate scale, one could read activity scores to the nearest eighth of a mile. Later, a second experiment was carried out in an analogous fashion with two additional experimental animals (not contained in Table 1) and two control animals. At the end of eight days, the new monkeys were each given a dose of 400 r.

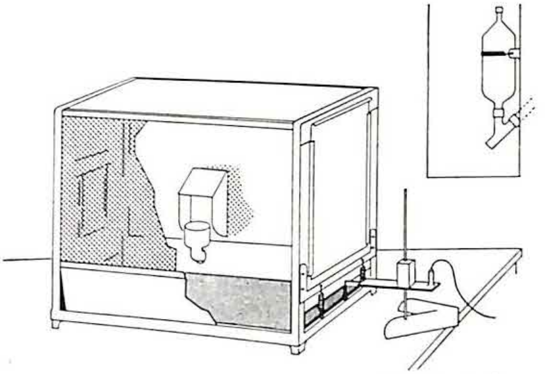

FIG. 1. Individual monkey cage with attached strain-gauge.

Weight-pulling. A portable weight-pulling apparatus, diagrammed in Fig. 3, was used in the 400 r. experiment. Weights of 500 gm. or 1000 gm. were added to a free-hanging pan, which was attached through a pulley system to the test tray, until the monkey failed to pull in the tray on three successive attempts. As incentive, a small piece of banana was placed in an open metal holder at a predetermined distance on the test board. Usually, one more piece of banana was added after a failure, but the monkey's last attempt was run with an additional piece several times the standard size. The pull was a short one, 7 in. to 9 in., depending on *S*'s reach, and the monkey was allowed to use both hands. A spring-loaded stop held the tray so it could not fall back after a successful pull. Generally, two or three tests were given (9:00 P.M. or 10:00 P.M.) each week, although in the early training period about one month before irradiation they were more frequent.

Irradiation technique. Animals were confined in a circular Plexiglas cylinder to whose shape the slightly scrunched-down monkey roughly conformed. This tube was hung by strings, 8 in. or more in length, from a

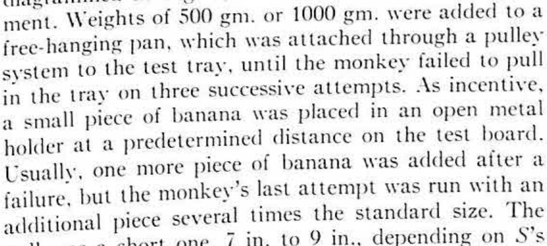

FIG. 2. Three-step mechanical puzzle and pedometer.

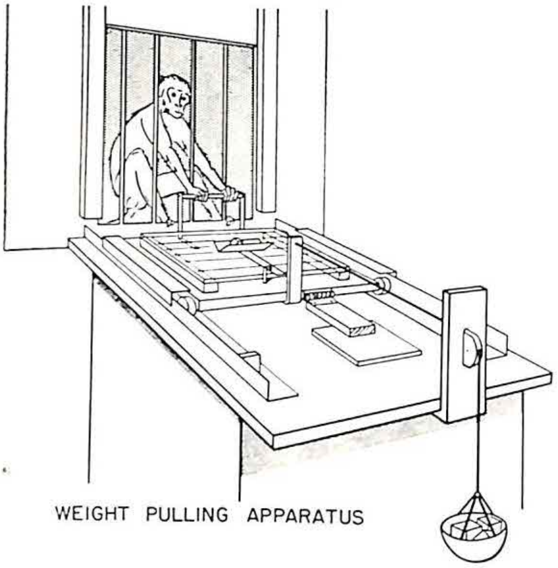

FIG. 3 Weight-pulling apparatus in use.

slender metal shaft which rotated it at 1 rpm in the center of a horizontal field of X rays. At all radiation levels except 400 r. the monkey was 5 ft. from the source and received about 5.0 r/min. air dose. In the 400 r. experiment, the *S*s were 4 ft. from the source, and the rate of delivery was about 7.2 r/min. air dose. Calibrations made with a Victoreen thimble chamber revealed that the dose in a Masonite phantom was at least 98.5 per cent of that found in air and that the maximal variation in dose within the space occupied by the monkey's body was not over 10 per cent at 4 ft. or 6 per cent at 5 ft. Throughout irradiation the *E* maintained the voltage at 200 kv. and the current at 15 ma. Filtration totaled 0.5 mm. Cu and 2.0 mm. Al. A number of control animals in each experiment were placed in the tube and rotated in front of the dead X-ray machine.

Treatment of data. All scores within a subgroup (see Table 1) were ordered in terms of the days by which they preceded or followed the day on which the experimental monkeys in this subgroup were irradiated. In averaging subgroups to obtain group means, the same system of aligning the data was utilized, so that exposure days coincided. A group mean for controls was obtained by entering each control subgroup mean once for each associated experimental *S*, taking their total, and dividing by their number, which was also the number of irradiated monkeys.

The number of control cases shown in Table 1 is correct for the postirradiation measurements except the strain-gauge activity recording of the 50 r. and 100 r. group, the 300 r. group, and the 400 r. group, where the total controls in each group were reduced to 0, 2, and 12, respectively.

Since irradiation, with one exception, occurred at the beginning of the week, the first postirradiation week has been taken as the remainder of that week. One 200 r. monkey was irradiated on a Thursday, and data gathered on the next two days were averaged to obtain the first postirradiation week mean.

RESULTS

Strain-Gauge Recorded Activity

Activity records were scored in terms of pen deviations which indicated a cage-crossing from back to front, or vice versa. There was no statistically reliable evidence of a decrease in this activity after irradiation. At 200 r. and again at 400 r., the relative decrease in activity was greater for the experimental animals than for their controls on the day of exposure and in the first postirradiation week. However, just the opposite trend appeared in the 300 r. group. It is possible that social interaction among the monkeys, which were in individual cages in the same room, tended to obscure irradiation effects.

Activity Ratings and Observations at 400 r.

Five general categories of behavior were selected: (*a*) movements from front to back of cage and vice versa; (*b*) climbing, standing, and unusual posturing; (*c*) scratching and grooming; (*d*) sitting or lying down; (*e*) chewing. Total rating scores were computed for each category, and differences were obtained between the mean scores in the postirradiation period and the mean scores in the week before irradiation. Subtracting the group mean of changes of controls from those of experimentals gave differences in each subgroup. The values obtained by combining subgroup scores are plotted in Figure 4.

Subgroup control and irradiated monkeys were compared by use of the Mann-Whitney test (14), and, using the technique cited by Fisher (4, pp. 99–101) for combining probabilities, we obtained chi squares with 6 *df* for

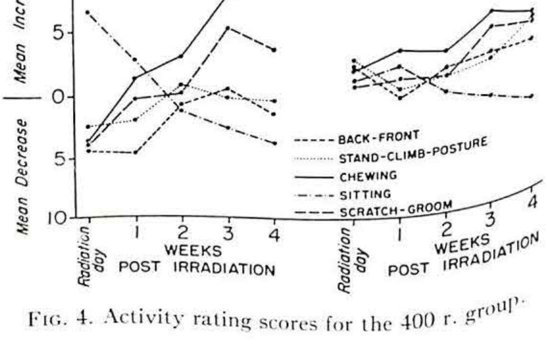

FIG. 4. Activity rating scores for the 400 r. group.

each category for the day of irradiation and for the first and second postirradiation weeks.

Only for the day of exposure were the one-tailed values of the chi squares less than .05. These *p*'s were .025, .04, and .05 for chewing activity, grooming and scratching, and back-front movements, respectively.

Unusual behavior after irradiation was not noticed in 50 r. and 100 r. monkeys, but all other experimental animals displayed varying degrees of transient immobilization or prostration beginning perhaps 30 to 60 min. after removal from the X rays. Definite recovery occurred in a few hours, but two 400 r. *S*s showed exceptional inactivity in the evening observation period, and one continued to assume a prone posture the following evening. Apart from pallor and a slight roughening of the coat, there were no characteristics by which a casual observer could identify irradiated monkeys.

Mechanical Puzzle Manipulation

Only the 100 r. and 50 r. group, and two experimental monkeys in the 300 r. group were tested on irradiation day within an hour or two after exposure. No change in score was noticed in the 100 r. and 50 r. group, but the 300 r. animals exhibited almost no manipulation tendency.

At all dosage levels above 100 r., the average changes recorded between the week before irradiation, and the first and second postirradiation weeks were more positive for the controls than for the experimental *S*s. However, none of the available comparisons afforded differences approaching statistical significance. It was noted that in each group, exclusive of the lowest dose group, there was one irradiated animal exhibiting a marked decrease in score lasting three weeks or more. In view of the consistency of individual performance and the recognized variation in individual susceptibility to radiation, this might be taken as evidence of a selective effect on manipulatory drive which appears in a minority of exposed animals.

Pedometer Manipulation

A different picture from that yielded by the mechanical puzzle was given by the pedometers, which were introduced with the thought that they would better meet the requirement of low motivation. Since day-to-day variability was large, extreme scores being occasionally recorded, medians rather than means were thought to be the more representative measure of performance. Median scores were obtained for the preirradiation period of eight days, and for blocks of eight days in the postirradiation period, excluding the exposure day. In Figure 5 the postirradiation scores are shown as percentages of the preirradiation score

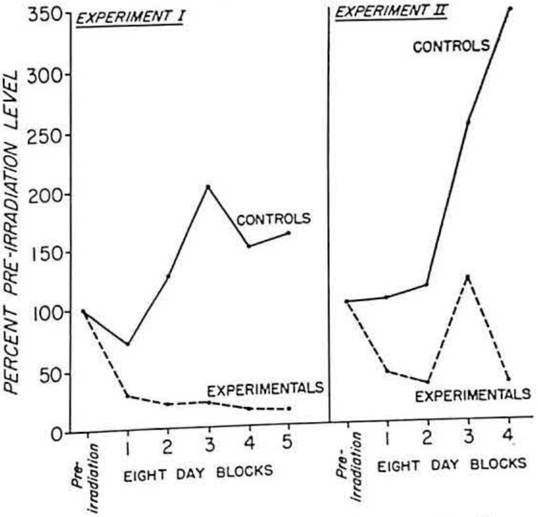

FIG. 5. Pedometer manipulation after a 400 r. dose.

In both the original experiment and the later experiment, the control animals increased their manipulations in the postirradiation period while the experimentals decreased their manipulations. Analyses of variance yielded *F*'s significant at the .05 level of confidence in both experiments.

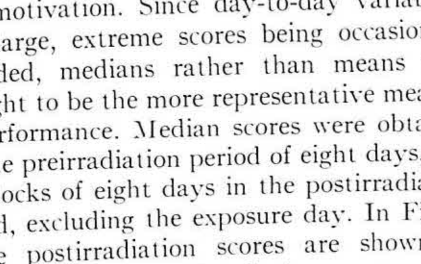

FIG. 6. Weight-pulling in the 400 r. group.

Weight-Pulling at 400 r.

Vigorous weight-pulling developed prior to irradiation was maintained in the postirradiation period, including the evening of the day of exposure, although in experimental *S*s a slight, statistically unreliable, decrement was found on radiation day and during the following week, as seen in Figure 6. Peak performance, which usually represented a pull of over three times the animal's body weight, was reached by all *S*s in the postirradiation period.

DISCUSSION

The results show no reliable decrement after irradiation day in the general activity, strength, or puzzle manipulation of monkeys receiving as much as 400 r. Since peak performance in the weight-pulling tasks demands both motivation and strength, we may assume that the rewarding or incentive value of a highly desirable food is little affected by sublethal irradiation. These negative findings must be qualified by *(a)* the small number of animals used at any dosage level, *(b)* the fact that a few individual animals seemed to show an irradiation effect, and *(c)* the lack of stability and the amount of variability found in activity ratings, especially during the first few weeks of testing.

The lowest weight-pulling score in the first postirradiation week, 89 per cent of normal pull, was made by an exposed animal, and on irradiation day the third subgroup yielded a t of 3.2, significant at the .05 level of confidence in a comparison of weight-pulling by control and experimental *S*s. At 200 r., 300 r., and again at 400 r., the monkey showing the relatively lowest manipulatory drive in the postexposure period was an irradiated monkey. Ratings of back-front movements in the 400 r. group show that an experimental animal had the biggest and most consistent decrement (true also of stand, climb, and posture ratings), and that there is a practically complete separation of control and irradiated monkeys in subgroups II and III on both the day of exposure and during the first week.

A re-evaluation of these results indicates that at least some *S*s exposed to 400 r. showed behavioral deficits. If the obtained mean differences were taken to be accurate, then the largest changes occurred in various categories of general activity and the smallest in weight-pulling. This result is entirely in keeping with the thesis stated at the beginning of the paper, namely that stress will affect low-motivation behavioral outlets rather than high-motivation strength and intelligence tests, but the foregoing evidence is insufficient to draw a definite conclusion.

Of greatest interest is the large and persistent decrement in pedometer manipulation, which was observed in four monkeys that received 400 r. It appears that the nature of the manipulation measured by pedometers differs from that elicited by mechanical puzzles. Observation suggests that pedometer manipulation embodies a rather low incentive value for the monkey, which is not apt to continue handling the apparatus uninterruptedly for more than perhaps 30 sec. On the other hand, the energetic and seemingly inexhaustible attack of the practiced monkey on the mechanical puzzle leads us to think that *S*'s motivation is not of the low order which was originally envisaged.

The conditions under which manipulation and activity are measured are no doubt of decisive importance. The utilized procedure of staggering the date of radiation, although tending to minimize any socially transmitted disturbance reflecting the stress or distress experienced by individual animals, would not eliminate it. That our irradiated monkeys showed no reliable change in strain-gauge recordings read for circumambulatory activity during evening or early morning hours does not mean that another method would not uncover some change. Both our observational ratings and those made by Davis[3] suggest that an activity effect exists. Persistent decrements in activity have been reported for the burro (16), following an initial 24 hr. in which the behavior was possibly "euphoric," and for the rat (8), which, however, displayed a transient amelioration of the hypoactivity at the mid-lethal but not the lower dose levels. Hagen *et al.* (5) described their irradiated rabbits as irritable and aggressive. Negative activity findings for monkeys in the early postexposure period have been reported by Kaplan *et al.* (11)

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[3] See footnote 2.

and by Eldred and Trowbridge (3), who believe that the monkey, like man, undergoes a latent period, but these investigators apparently did not use quantitative procedures. It is likely that in the low-level radiation syndrome there are relatively few of the overshadowing delayed reactions which follow severe exposure.

Despite the indications of decreased activity in our *Ss*, they were by no means incapacitated. The actual activity and the weight-pulling ability of the 400 r. animals suggest a less sick and more vigorous organism in the latter part of the postexposure month than do descriptions of men (1, 2, 7, 12) or burros (16) irradiated with a comparable dose (approximately two-thirds of the $LD_{50/30}$ dose). Clinical observations attest that human atomic radiation victims often experience prostration on the first day, enter a relatively symptom-free period of several days or weeks, which may not be a period of real well-being (7, 13), and then undergo a delayed (sometimes acute) reaction. Weakness and fatigability may be prolonged. Apart from pedometer manipulation, a sustained effect was not seen in our *Ss*.

SUMMARY

Groups of two, six, and five monkeys received whole-body X-ray doses of 200 r., 300 r., and 400 r., respectively. Six animals were re-irradiated with 50 r. or 100 r. The number of control monkeys at different dose levels varied. Strain-gauge recordings of general activity and a mechanical puzzle manipulation test were carried out with all animals; observational ratings of behavior and a weight-pulling test were utilized only at 400 r. Decreased activity was not found on the evening of radiation day except in the ratings of 400 r. animals, although monkeys treated with doses of 200 r. or more showed transient inactivity and listlessness shortly after exposure. Since a striking and prolonged decrease occurred in a pedometer-manipulation test carried out with four of the 400 r. animals, two new monkeys and two controls were subjected to an identical procedure. The same result was obtained. There was some indication that weight-pulling ability, activity rating scores, and puzzle manipulation were affected in the early postirradiation period in individual animals receiving 200 r. or more. The results lend support to the hypothesis that lightly motivated behavior is more susceptible to stress than is highly motivated behavior.

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FOOD-PREFERENCE CHANGES OF MONKEYS SUBJECTED TO LOW-LEVEL IRRADIATION[1]

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It is known that most irradiated animals exhibit anorexia after whole-body irradiation, and that some proportionality exists between the size of the dose and the extent of the reduction in food consumption. Little is known concerning the effects of radiation on the palatability of specific foods, and it is with this problem that the present study deals.

METHODS

Subjects and Irradiation

Both the 18 young monkeys and the irradiation schedule and procedure are described in the preceding article (3).

Food Preference Test

Training in food preference began three weeks or more before exposure and was continued three or more weeks afterward. In most cases three to five preference tests were given each week although in a few instances only two tests occurred. The test apparatus is illustrated in Figure 1. It was mounted on a cart and placed in front of an animal's cage. The cage door was raised so *S* could reach out through a set of bars which were fastened to a wooden frame. The *E* placed the two preference foods in wells on a sliding tray while the opaque screen was down. Next, the screen was raised. The tray was pushed forward, and the monkey was permitted to obtain one of the foods. Twenty-four choice trials were conducted at one time. The left and right positions of the foods were determined by three random sequences in which each food appeared equally often on each side. Four foods, uniformly prepared, were used—apple, carrot, raisin, and peanut for the 50 r. and 100 r., 300 r., and 400 r. groups; apple, carrot, raisin, and bread for the 200 r. group. From four different items, six unique pairings are possible, and four replications of these were utilized at one testing. Thus any particular food was presented during 12 trials, but it was paired with any other food only four times.

RESULTS

In interpreting the results it must be kept in mind that the nature of the preference test limited the size of change which could be recorded. An animal had to choose one of a pair of foods on four presentations even though it had a low regard for both, and an animal could increase choices of a particular item only to the extent that there were choices in the past on which it had passed up this item. A shift on one trial from the previous choice to a new choice is regarded as a single preference change although it was doubly recorded—once as a gain and once as a loss.

It was feasible to run *t* tests only on the subgroup preference changes at the 400 r. level because animals irradiated at the other levels either showed no appreciable change or were bracketed with too few controls. The means of the differences in choices between the week before and the week after X-ray exposure yielded a *t* of 2.6, significant at the .05 confidence level, for the comparison of controls and experimentals in subgroup I. The comparison in subgroup II yielded a *t* of 11.3, significant at the .001 level of confidence. In subgroup III only one experimental animal exceeded its controls in preference shifts, and *t* lacked significance.

That there was no obvious relationship between size of dose and number of shifts in food preference can be seen in Figure 2. Here are plotted the differences between the percentages of changes recorded for experimental and control animals, with the first week before irradiation taken as the standard (zero change point) for all animals. As previously described (3) scores have been averaged as if all animals at a given dose level were irradiated on the same day. A value above zero indicates that the shift was larger for the exposed monkeys, and a value below zero indicates that the shift was larger for the controls. The mean change for the control groups generally ran between 6 per

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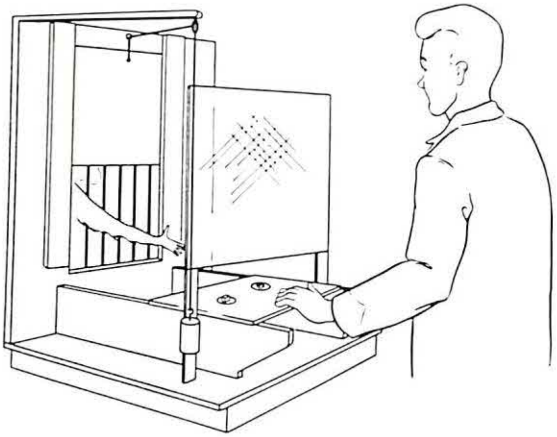

FIG. 1. Food preference testing apparatus.

cent and 13 per cent, and the actual changes for the experimental groups were often considerably higher. Thus, in the first postirradiation week the irradiated 200 r. monkeys registered a mean change of 29.5 per cent and the irradiated 400 r. monkeys, 19.7 per cent.

It was possible to test a number of the monkeys shortly after they had received the radiation dose. No disturbance was found at 50 r. or 100 r., but one 200 r. animal refused food during four presentations (bread and raisin), and three of the four animals in the 300 r. group which were tested at this time refused food 20 times or more. Food rejection was still more striking in the 400 r. group; three tested *S*s made a total of 7 choices out of a possible 72. On all subsequent test days, nearly complete cooperation was secured from all monkeys. That the refusals on radiation day were not due to any stress resulting from confinement in the Plexiglas tube was shown by several controls that were subjected to the entire irradiation procedure excepting actual exposure to X rays.

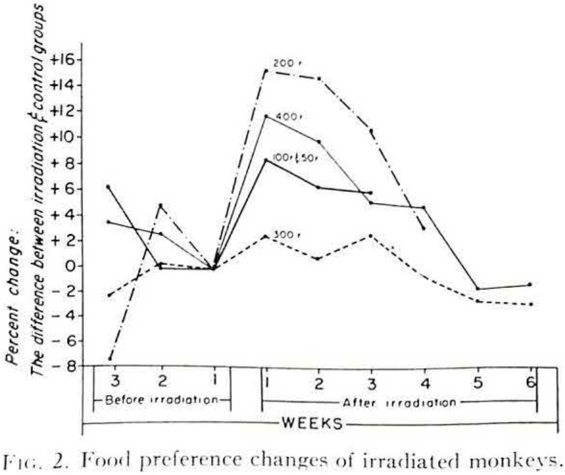

FIG. 2. Food preference changes of irradiated monkeys.

Generally, a return to normal preference habits occurred by at least the fifth week, as indicated in Figure 2, and an examination of individual cases shows that several monkeys were back within the normal range by the third postirradiation week. Sustained shifts were still in evidence for two animals at the termination of testing: one 200 r. monkey in the sixth week and one 100 r. monkey in the third week.

Individual differences in the food preference changes of the two *S*s in each group that showed the greatest radiation effect are shown in Table 1. A general pattern may be delineated in terms of animals' increasing or decreasing choices of a particular item going from the first preirradiation week (week −1) to the first postirradiation week (week +1). The majority of monkeys increased apple choices (5 gains, 2 losses, 1 no change) and carrot choices (8 gains), and decreased peanut choices (7 losses, 1 no change), while their raisin choices were roughly stable. An examination of those 11 cases which exhibited smaller preference shifts, and therefore lie outside the table, confirms the picture of apple increase (5 gains, 2 losses, 4 no changes) and peanut decrease (7 losses, 2 gains, 2 no changes), but reveals no dominant tendency regarding carrot (3 gains, 3 losses, 5 no changes) or raisin (6 gains, 4 losses, 1 no change). Such trends are not found among the controls where in 28 cases the gains for peanut (or bread), carrot, raisin, and apple were 11, 13, 13, and 11, respectively, and the losses were 16, 12, 13, and 14, respectively.

DISCUSSION

Although variations in preference do occur in normal monkeys, they are usually of small magnitude, and the obtained ratios for choice afford a fairly stable standard against which changes induced by experimental variables may be measured. The lawfulness of the preferences made by monkey *S*s has been demonstrated by Harlow and Meyer (2), who found that the preference for larger over smaller amounts of the same food could be predicted from a logarithmic scale of quantity, and by

TABLE 1

Average Weekly Choices

Radiation Dose (r.)	Subject	Weeks							
		−1	+1	+2	+3	−1	+1	+2	+3
		Apple				Peanut*			
100	O	5.0	1.7	3.3	4.0	11.0	7.0	6.3	5.0
100	F	0.0	4.7	5.3	2.0	8.0	2.0	5.3	10.0
200	G†	4.8	9.3	9.8	6.8	9.6	1.5	1.0	3.0
200	F	7.0	12.0	9.1	8.2	0.0	0.0	0.0	0.0
300	T	1.5	1.0	1.0	0.3	11.5	9.7	10.3	9.7
300	SNE	2.8	5.7	2.3	3.5	10.5	2.3	7.3	9.5
400	S	5.8	8.8	10.8	8.8	10.8	8.3	7.4	4.6
400	J	3.2	9.3	9.4	5.2	5.8	5.0	3.0	5.0
		Carrot				Raisin			
100	O	0.0	3.7	3.0	3.0	8.0	11.7	11.3	12.0
100	F	4.0	5.7	1.3	2.0	12.0	11.7	12.0	10.0
200	G†	4.8	7.5	6.0	2.5	4.8	5.3	7.3	11.3
200	F	6.7	8.0	4.8	5.0	10.3	4.0	10.0	10.8
300	T	3.0	3.3	3.7	4.3	8.0	10.0	9.0	9.7
300	SNE	1.5	4.0	2.7	0.5	9.3	12.0	11.7	10.5
400	S	0.2	5.3	4.8	9.0	7.2	1.8	1.0	1.6
400	J	5.6	7.8	8.2	5.0	9.4	2.0	3.4	8.8

*Bread instead of peanut was used for 200 r. monkeys.
†Refused to make selection on some trials.

Fay, Miller, and Harlow (1), who found that the percentage of choices of qualitatively different foods could be shifted in a regular fashion according to quantitative ratios.

There appeared to be a relationship between size of X-ray dose and number of refusals made on the day of irradiation, but an uncontrolled variable, namely, the temporal separation of the test from exposure, is undoubtedly of importance. Informal observations indicated that food aversion and, occasionally, nausea set in by the end of the first hour when the dose was 200 r. or more.

The results of food intake measurements (unpublished) indicate that eating decreased in all groups (except perhaps the 50 r. and 100 r. group) during the first postirradiation week. Excluding tests made shortly after exposure, anorexia did not extend to the preference foods, nor to an evening supplement of banana, which was consumed by all 400 r. monkeys, even on the night of radiation day.

Food intake differences between control and experimental *S*s disappeared in the second week, when the dose was 300 r., but probably lasted several weeks more after 400 r. It was interesting to note some disparities between food intake reduction and food preference shifts. Two monkeys—G and F—irradiated at 200 r. and 100 r., respectively, were clearly at or above their normal food intake during most of the postirradiation period but showed major and continued preference changes (Table 1). Monkeys SNE and S, having received doses of 300 r. and 400 r., respectively, showed some changes in food choices, but little or inconsistent reduction in food intake. On the other hand, there were *S*s who showed reduced food intake and no appreciable change in preference; this phenomenon was most striking in the 300 r. group. The evidence points to the conclusion that a selective anorexia (or possibly a selective appetite) may be induced independently of variation in general hunger.

There is evidence that variation in hunger produced by changes in the length of the deprivation interval does not affect the preferences of monkeys (2) or rats (4, 6). In one study (5), rats that developed bronchopneumonia tended to react with indifference in a food-choice situation, but their relative preferences remained unchanged. Our monkeys showed decided preferences throughout the period of radiation sickness, during which drastic changes occurred in the blood pictures of those receiving doses of 200 r. or more.

The lack of effect found in four or five of the six animals given 300 r. creates a problem. One hypothesis is that the preference habits inculcated by practice were especially strong in these monkeys. The resistance to change in preference has been amply demonstrated in the rat by P. T. Young (6). However, even in the 300 r. group a detailed examination of the data over the period of two days before to two days after exposure reveals a decrease, usually slight, in peanut choices in five of the six experimental animals. It is likely that with improved test procedures food-preference changes could become a very sensitive index of radiation effect.

With the particular foods involved there appears to be a shift from high-caloric foods (peanut, bread) to low-caloric foods (apple, carrot). This could be linked to a decreased food intake if food intake and preference did not, as pointed out above, display independent variation. The particular shift found is also a shift from dry to moist food. The latter may be preferred because of dehydration.

SUMMARY

Free choices between four foods—apple, carrot, raisin, and peanut (or bread)—presented two at a time—were allowed rhesus monkeys both before and after whole-body irradiation. Initial and persisting changes in preference were found in individual monkeys after doses ranging from 50 r. to 300 r.; after 400 r. the difference between control and experimental *S*s was statistically significant. Generally, apples and/or carrots were chosen more often after treatment and peanuts less often. It was noted that changes in food intake and in food preference did not always accompany each other. A return to normal occurred in most *S*s by at least the fifth week.

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THE FUNCTION OF THE MEDIAN CEREBRAL CORTEX IN MATERNAL BEHAVIOR OF RATS[1]

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The median portions of the cerebral cortex of the rat seem to have important functions in the animal's hoarding activity. In a previous investigation (6) it was found that rats, after ablations of these cortical areas, accumulated significantly fewer pellets during hoarding trials than they had done preoperatively, whereas the hoarding performance of rats with lateral ablations of similar dimensions was approximately the same in pre- and postoperative trials. Ablations of the median cortex affected the amount of pellets accumulated but did not greatly influence other measures of hoarding activity, such as the onset, latency, or speed of hoarding.

Since hoarding activity is, at least partly, an innate behavior pattern, it is probable that the median cerebral cortex also performs an important function in other patterns of unlearned behavior. The maternal activity of rats is a complex, well-integrated behavior pattern, which has been extensively investigated by Sturman-Hulbe and Stone (8) and by Wiesner and Sheard (9). Beach (1, 2) and Stone (7), who investigated the effects of cortical lesions on maternal behavior of rats, found impairment of several aspects of this behavior, such as cleaning and gathering of pups after parturition, nest construction, and retrieving of the litter. Deterioration of these patterns increased as a function of the magnitude of the cortical ablations, provided they were larger than 10 per cent and less than 40 per cent of the total neocortical surface. Lesions of larger dimensions resulted in almost total loss of maternal behavior. In Beach's investigation (1) the group of rats with lesions between 10 per cent and 20 per cent of the cortex showed only small changes in patterns of maternal activity.

In the present investigation it was attempted to produce relatively small ablations, less than 20 per cent of the total neocortex, along the median cortex of rats and to compare the maternal behavior patterns of these animals with those of rats which had lesions of similar dimensions along the lateral cortical areas, and with unoperated rats.

METHOD

Subjects

The *S*s were albino rats (210 to 290 gm.) which had delivered one or two litters each prior to the experiment. Three groups of *S*s were used: control rats (C group), which were not subjected to brain operations, rats with bilateral ablations of the median cortex (M group), and those with bilateral ablations of the dorsolateral cortical areas (L group). The experimental *S*s were subjected to operative procedures similar to those previously described (6), except that the cortical tissue was removed by aspiration. Each operated *S*, after it had fully recovered (at least 14 days after surgery), was placed with a male albino rat. If an *S* did not appear pregnant two weeks after mating, it was remated with a different male after an intervening rest period of one to two weeks. The groups of *S*s consisted of 11 rats in the C group, 12 in the L group, and 16 in the M group. Three additional rats had lateral lesions of considerably larger dimensions than those in the L group and are considered apart from the *S*s in group L.

Procedure

The observation box. Several days prior to parturition, as judged by the extension of its abdomen, the *S* was placed in an observation box. This box consisted of two compartments, each 17 in. by 22 in., which were connected by a 4-in.-wide passage. The box was 10 in. high, and its sides and two hinged tops consisted of panels of wire screening. A bin containing Purina Laboratory Chow pellets was placed in one corner along the partition of one compartment, and a water bottle was placed above the bin. Forty strips, $1\frac{1}{2}$ in. by 9 in., cut from paper towels, were scattered on the floor of the other compartment. The required number of observation boxes were placed in a basement room which had a temperature between 70° and 78°F.

Parturition. It was attempted to observe each *S* as soon after parturition as possible, at least within 12 hr. The place of parturition, the number of live and dead pups, the removal of fetal membranes, and the general appearance of cleanliness of the pups were recorded. The quality of nest construction and the degree to which the *S*'s litter was gathered in the box were rated.

Pup replacement. The number of live pups in each

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[1] This investigation was supported by a research grant from the Hixon Fund. The author wishes to express his appreciation to Miss Ruth E. Estey and to Mrs. E. Scheurenberg for their continued assistance during this investigation.

litter was recorded daily. Since most of the litters of *S*s in group M did not survive more than a few days, they were replaced by foster pups. During preliminary experiments it was observed that lactation could be induced in rats with median lesions by introducing foster pups one day after parturition, provided the pups were two to four days old. The rats would generally not lactate if the foster pups were placed in the box two or three days after parturition, or if younger pups were introduced on the first day *post partum*. Foster pups were used only when a large portion of an *S*'s litter had died on the first day after birth. Additional foster pups were added to an *S*'s litter on subsequent days in order to maintain a litter size between five and nine, and preferably seven pups. Some *S*s in the C group had pups removed when their litters were large and no other foster pups were available.

The fan tests. On the first day *post partum*, i.e., between 12 and 36 hr. after birth, a 10-in. electric fan was placed outside the observation box near the nest, and the air blast was directed against the nest for a period of 1 hr. If the nest was so compact that the air blast did not destroy it, the paper strips and pups were scattered by *E* after the fan had been running for 5 min. The blast was sufficiently strong to make it impossible for *S* to rebuild its nest in the original place. Similar fan tests were conducted on the second and third days *post partum*.

The heat tests. On the fourth and fifth days *post partum* a 645-w. radiant-type electric heater was placed outside the observation box near the litter for periods of 1 hr. During preliminary trials it was observed that pups which remained exposed to the heat could survive only from $\frac{3}{4}$ to a maximum of $1\frac{1}{4}$ hr. When the rat did not move its pups from the heat, they frequently were able to crawl away themselves. If this occurred during the first $\frac{1}{2}$ hr. of the heat test, the pups were returned to the heated area by *E*.

The behavior of *S* was observed during the course of each fan and heat test and was recorded at intervals of 5 or 10 min. Records were kept of behavior patterns such as: the carrying of strips or pellets by the rat, nest-building, carrying and depositing of pups, the *S*'s running and resting behavior, and the distribution of pups and paper strips on the floor of the observation box.

Termination of the experiment. On the day after the last heat test the quality of nest construction and gathering of pups were recorded. The rat and its litter were then removed from the box.

The operated animals were killed by perfusion with 95 per cent alcohol solution. The brains were then removed, fixed in alcohol, and imbedded in paraffin. They were sectioned at $25\ \mu$, and every twentieth section was mounted and stained with gallocyanin. The lesions were reconstructed on standard Lashley diagrams, and the size of the lesions was determined with a planimeter.

Rating Scales

Nest construction scale. The type and quality of the nest which each rat had constructed was recorded daily, starting with the first day after the rat's placement in the box, and at intervals during the fan and heat tests. The quality of nest construction was rated according to the following six-point scale:

0—The rat made no use of the nesting materials at all; the strips remained where they had been scattered by *E*.

1—The rat moved a few strips on a floor area corresponding approximately to one-half of one compartment. During a test only one or several strips were moved.

2—The strips were assembled for a simple floor covering in a limited area of one compartment, but there was no nest construction.

3—A crude nest was assembled. Most of the strips were used, some were torn, and they were arranged in a limited floor area. The rating was also applied when two or more small nests were constructed in different corners of the box.

4—A real nest, using all the paper strips, was constructed. The strips were torn, the nest appeared compact, with a good flooring and solid sides.

5—An excellent, compact nest was constructed. Food pellets were used to strengthen the sides of the nest, so the airblast could not blow it apart. Generally, all available materials, including the smallest paper strips, food pellets, and even feces were used in the nest structure, and the floors of both compartments appeared very clean.

The process of the construction of a 4 or 5 nest followed the pattern of nest-building described for a normal rat (4). The rat first assembled most of the available nesting material into a high pile in one corner of a compartment (some control rats, after the first fan test, had pushed the food bin underneath the passage between the compartments and built the nest there); it then made a depression in the center of the pile, and finally improved the construction of the sides of the nest, adding to the structure additional nesting materials, such as fine paper strips, food pellets, or feces.

Gathering scale. The degree of scattering or gathering of the rat's litter was evaluated according to the following four-point rating scale:

0—The litter was scattered over the floor of one or both compartments.

1—The litter was scattered over approximately one-half the floor area of one compartment, or some pups were placed underneath the paper strips of the nest where they were crushed to death. The rating was also applied when the pups were placed in several clusters in the observation box.

2—Some pups were in the nest, while others were nearby. Sometimes one pup was at a distance from the nest.

3—The whole litter was closely assembled in a compact pile, usually in the nest. This pattern is characteristic for the normal rat (4).

RESULTS

Cortical Lesions

Figures 1 and 2 show the reconstructions of the lateral (group L) and the median (group M) lesions, respectively. The size of

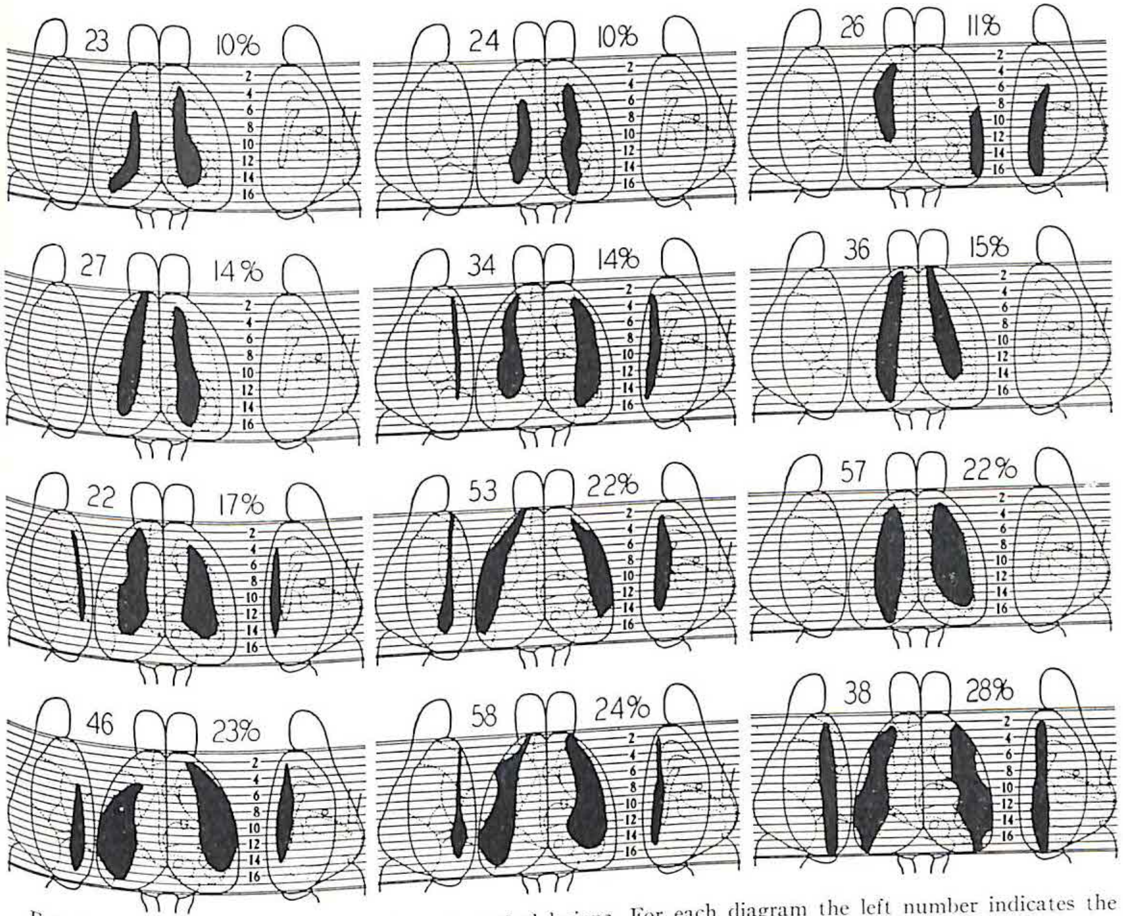

FIG. 1. Reconstruction of the dorsolateral cortical lesions. For each diagram the left number indicates the identification of the animal, the right number the percentage of cortex removed.

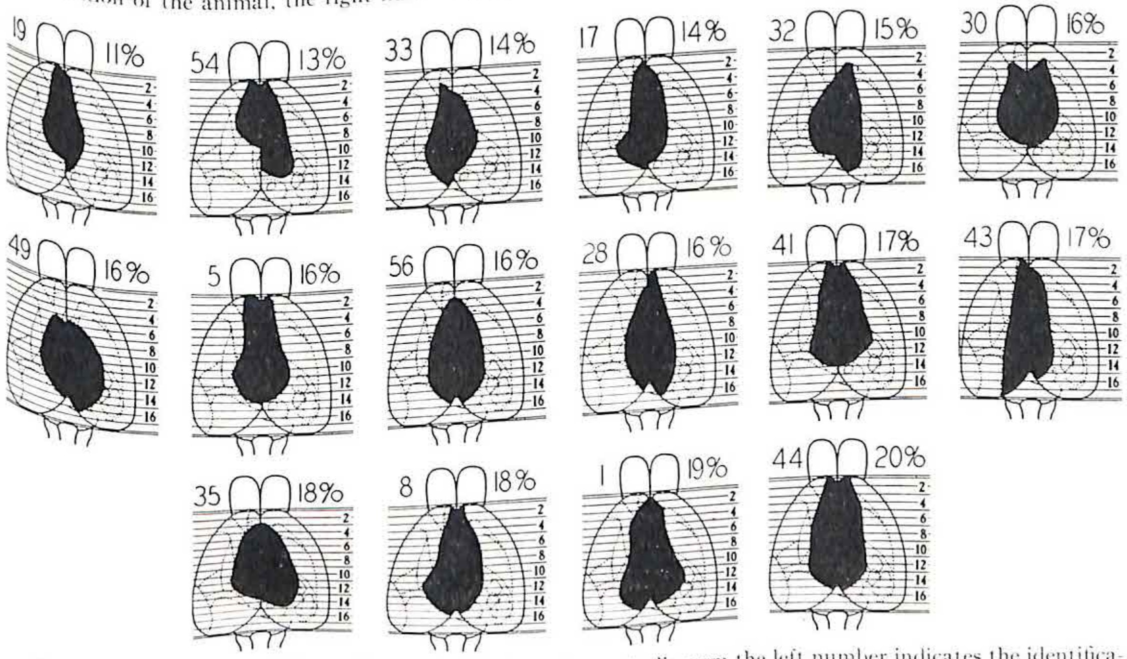

FIG. 2. Reconstruction of the median cortical lesions. For each diagram the left number indicates the identification of the animal, the right number the percentage of cortex removed.

the lateral lesions was between 10 per cent and 28 per cent of the cortical surface, the mean was 17.5 per cent, and the median of these lesions was 16 per cent. The size of the median lesions was between 11 per cent and 20 per cent, the mean was 15.8 per cent, and the median for this group of lesions was 16 per cent of the cortex. It was attempted to produce lesions of approximately the same area and length for the two groups of *S*s. However, five rats in group L had lesions between 20 per cent and 28 per cent.

It was more difficult to reconstruct the lateral lesions, because connective tissue, which developed across the ablated areas, often pulled on the edges of the surrounding cortical tissue. Sometimes the width of these lesions appeared smaller than the inside diameter of the glass pipette, used for aspiration of the tissue. This effect tended to result in underestimates of the size of the lateral lesions, which was not critical, however, since the *S*s with lateral lesions were to serve as a comparison group, with ablations of equal or somewhat larger dimensions than those of the M group.

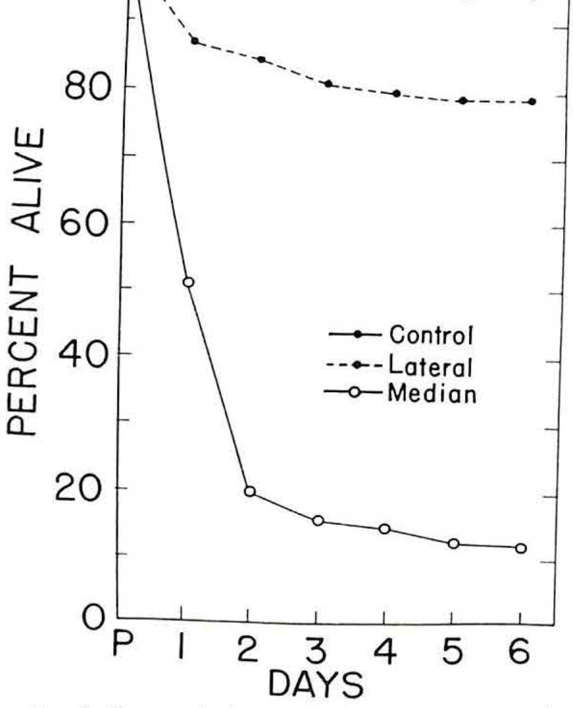

FIG. 3. Pup survival on successive days after parturition (day P). The ordinate indicates the mean percentage of litters surviving.

During aspiration of the cortical tissue the underlying white matter was sometimes damaged, particularly above the lateral ventricle. An examination of the brain sections showed that in 7 *S*s of Group M there was some damage to the corpus callosum, generally only along the anterior portions of this structure. In rats no. 1, 32, and 56 some unilateral damage to the caudate nucleus was also noted along the dorsomedial surfaces of its anterior portions. This damage, however, was never extensive, and these *S*s exhibited no unusual behavior patterns. The histological sections were not examined for retrograde degeneration.

Survival of Pups

The mean size of the litters at birth was 9.0 pups for the C group, 9.8 for the L group, and 9.3 for the M group, which indicates no important differences between these groups. When the litters were first observed, almost all the young of the C and L rats were well cleaned and breathing. Most of the pups of every *S* in group M were also alive and breathing at that time, although a few were already dead. The placentae of all pups observed had been removed and the pups appeared reasonably clean.

Figure 3 shows the mean percentage of the litters of each of the three groups of *S*s which were alive on successive days after parturition. Eight control rats maintained litters intact throughout the experimental period, each of two rats lost one pup, and one rat lost five pups from a litter of nine during this time. Rats with lateral lesions showed considerable variability in the survival of their young, although on day 6 the mean survival was 79 per cent. Rats no. 24 and 26 had a survival of only two pups each from original litters of 6 and 7, respectively, and each of rats no. 22, 23, and 36 had lost approximately 50 per cent of its litter at the end of the experiment. None of the other *S*s in this group lost more than one pup during the experimental period. The loss of pups does not seem to be related to the extent of the cortical lesions.

Of the 16 rats in group M only no. 44 was able to keep all its litter of 13 alive during the experimental period, and no. 5 kept 5 pups from its litter of 7 during this time. On the other hand, all pups from 11 *S*s in this group had died on the second day *postpartum*. Using a criterion of 70 per cent of pup survival on day 6, comparisons between the *S*s in the C and L groups yielded a chi-square coefficient of 2.0 ($p > .10$, using Yates' correction for continuity), whereas the corresponding coefficient between the C and M groups was 12.6 ($p < .01$). These coefficients indicate that the difference in survival of pups between the C and L groups was statistically not significant, whereas that between the C and M group was highly significant.

It was observed that the *S*s with median lesions generally did not nurse their litters, but rested in places distant from the pups. However, foster pups which were at least two days old hung on to the nipples of the rat, even as it ran around in the box, and they were thereby able to induce lactation in *S*. Fourteen rats in group M received foster pups on the first and on subsequent days after parturition. Only 2 of these rats lost 1 foster pup each during the experimental period, except for pups killed during the fan and heat tests. A total of 89 foster pups was given to these *S*s, of which 87 survived on the fifth day after they were placed in the box. On the other hand, of the 149 pups which were born to the 16 *S*s in group M, only 23 survived on the fifth day *post partum*. These data indicate that death of the rat's own pups was not due to its inability to lactate, but rather because the *S* did not permit its young to suck on its nipples. The foster pups, by hanging on to the rat's nipples, were able to induce lactation in *S* and consequently were able to survive. At the termination of the experiments these foster pups appeared healthy and as big as their litter mates which had remained with their natural mothers. It was observed that pups which were not nursed died between two and four days after they had been removed from their mothers.

Nest Building

Figure 4 shows the mean ratings of nest construction for the three groups of *S*s on successive days prior to and after parturition. During the latter period the ratings were taken before each test, when the maximum ratings were observed for the day. The control animals started to build loose nests several days before parturition and constructed excellent nests during the *postpartum* period. During the fan and heat tests they rebuilt their nests in places distant from the disturbed area. Rats with lateral lesions differed from the control *S*s in their nest-building activity mainly during the preparturition period. After parturition their nests were constructed as well as those of the controls.

The continued improvement in nest construction after parturition of the C and L groups may be related to the destruction of the nests by the air blasts. It was observed that many *S*s in these groups built nests rated 5 after the first destruction of their nests by the blast. While constructing their nests, these rats frequently placed food pellets upon layers of paper strips which reinforced the walls of the nests, so that the air blast could not destroy them.

The quality of nest construction of rats with median lesions was greatly inferior to that of the other groups of *S*s. Although *S*s in group M used paper strips as a floor covering on the days after parturition, they were unable to construct real nests. Rat no. 44 obtained one rating of 4, while three other rats constructed a few nests rated 3. The

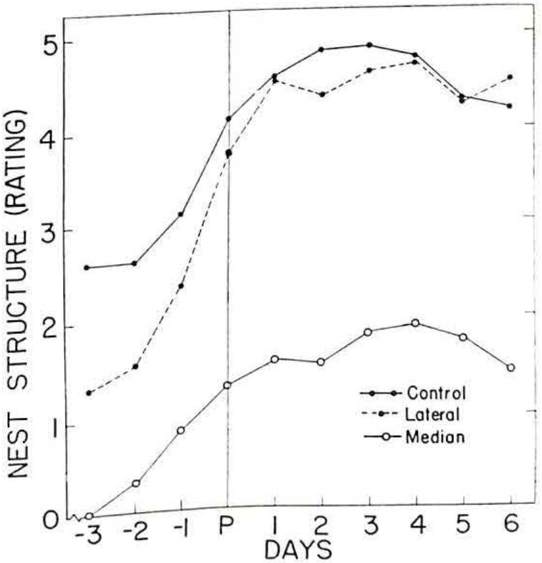

Fig. 4. Mean nest construction before (negative days) and after (positive days) parturition for the three groups. The rating scale is defined in the text.

maximum ratings for the nest structure of the remaining *S*s in this group was never higher than 2. Moreover, as seen in Figure 4, no *S* in group M made any use of the paper strips until two days prior to parturition (when only four *S*s began to move strips), and the mean rating on the day of parturition was only 1.3.

Collection of Pups

The normal, unoperated rat usually keeps its young in a compact pile in the nest, hovers over them, and permits them to nurse. This type of behavior is expressed by a rating of 3 on the Gathering Scale. As seen in Figure 5, this behavior pattern was expressed by all rats in group C and by most *S*s in the L group. In order for pups to be able to nurse and to survive, a gathering rating of at least 2 is required.

After parturition the litters of group M were generally distributed over the floors of the observation box. On the day of parturition and on the first day *post partum* only 3 of the 16 *S*s with median lesions obtained ratings of 2 or 3. The curve of daily gathering for the M group, as seen in Figure 5, shows a continuous increase after parturition and on day 4, when the mean group rating was 2.4, only two rats obtained ratings of 1, and no *S* obtained a 0 rating. The higher ratings may be the consequence of the introduction of foster pups and the consequent lactation by the *S*s. During this period the *S*'s behavior had undergone marked changes. Whereas before and shortly after parturition it frequently ran around the observation box in an aimless manner or rested at a distance from its young, the rat subsequently hovered over its litter during long periods of the day.

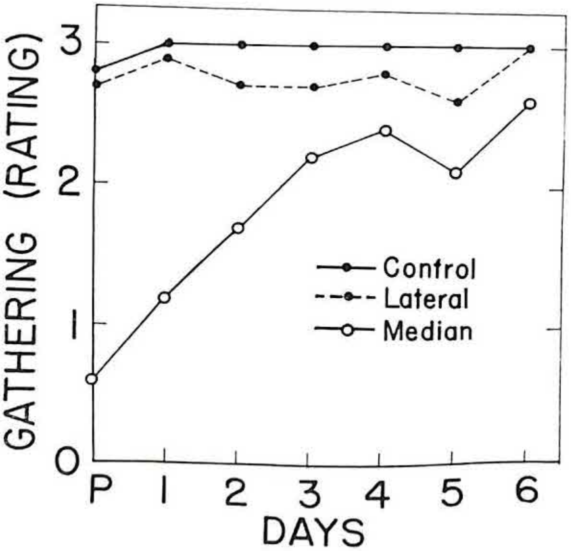

FIG. 5. Mean ratings of gathering of litters for the three groups on successive days after parturition (day P). The rating scale is defined in the text.

Response to Air Blast and Heat

In response to destruction of their nests by the air blast most control *S*s moved the nesting material to one corner in the undisturbed compartment, constructed a new nest there, and finally placed their pups in the new nest. During the third fan test, for example, ten control *S*s acted in this manner, and the remaining rat rebuilt its nest in the compartment where it was previously, but outside the area of the air blast. These rats spent the major portion of the hour-long test periods on rebuilding their nests and had usually constructed adequate nests at the end of the hour.

The *S*s in group L frequently did not move the nest materials to the undisturbed compartment but attempted to rebuild nests within the air blast. Even during the third fan test only 6 of the 12 rats in group L succeeded in constructing nests in the undisturbed compartments. The other *S*s attempted to reconstruct the nests in the area of the blast and only finally built nests in quiet corners of the same compartment. These animals were very active in moving strips, and often ignored their pups until they had succeeded in constructing new nests.

The rats with median lesions were little concerned with nest-building activity and therefore moved pups from the blast area soon after the start of the fan test. During the first 5 min. of the third fan test, for example, the *S*s in group M had moved 46 per cent of their litters from the air blast, whereas the *S*s in groups L and C had moved only 5 per cent and 6 per cent of their litters, respectively, at this time. The *S*s in the M group, however, did not systematically carry their young to safe places, but they ran aimlessly around the box, usually carrying pups, and eventually deposited their young on all parts

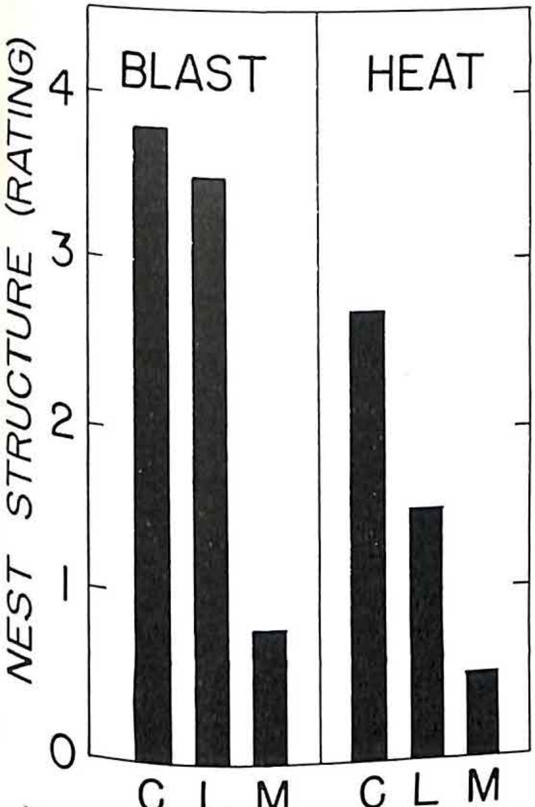

FIG. 6. Mean ratings of nest structure for the three groups at the end of the hour-long tests. Ratings are the means for the three fan tests and the two heat tests, respectively. The rating scale is defined in the text.

of the floor area. They frequently dropped pups again underneath the air blast.[2] At the end of the third fan test the mean percentage of litters moved from the blast area was 85 for the M group, 67 for the L group, and 88 for the C group.

The quality of nest construction at the end of the fan tests is shown in Figure 6, which indicates that *S*s in the L and C groups had succeeded in constructing useful nests during the hour-long tests, whereas the *S*s with median lesions had moved only a few strips. Figure 7 shows the ratings of gathering of litters for the three groups of *S*s at the end of the tests. It is apparent that the *S*s with median lesions, although they spent little time on nest construction, did not gather their litters as well as did the *S*s in the L and C groups.

The hour-long fan test was generally not fatal to pups which remained in the blast. None of the young of *S*s in the C and L groups was killed by any of these tests, and only 3 per cent of the litters of the M rats were killed during the first air blast test, 1 per cent during the second, and none during the third test.

During the heat tests the rat had to move its young to safe places, if they were to survive. During the second heat test, for example, all young of the control animals had been moved within 45 min., and 93 per cent of the L group's litters had been brought to safety within 1 hr. At this time 21 per cent of the M group's litters were still exposed to the heat. The aimless running behavior of a rat with median lesions is also expressed by the *S*'s "retrieving time," i.e., by the time interval between the rat's moving the first and the last pup of its litter to a safe place. The retrieving time for a control animal was never more than 15 min., 6 of the 12 *S*s in the L group retrieved their litters within this period, and all *S*s in this group had

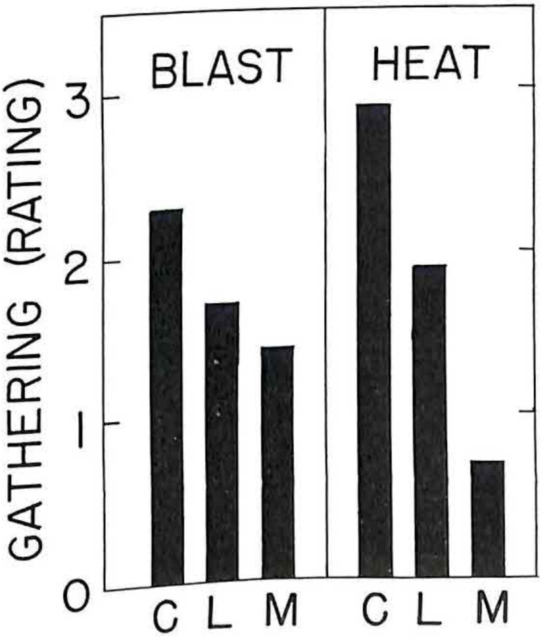

FIG. 7. Mean ratings of gatherings of pups for the three groups at the end of the hour-long tests. Ratings are the means for the three fan tests and the two heat tests, respectively. The rating scale is defined in the text.

[2] The marked difference in behavior between the normal and experimental *S*s is shown by a film (16 mm., color, silent), which may be obtained from the Division of Biology, California Institute of Technology, Pasadena, Calif.

brought their young to safety within 60 min. after they started retrieving. Although all rats in group M moved some of their pups from the heated area, only 10 *S*s had retrieved all their litter during the second heat test. The significance of the differences in retrieving time between groups of *S*s was determined by chi-square coefficients for a criterion of 15 min. This coefficient was 5.64 ($p < .02$, using Yates' correction for continuity) between the C and L groups, and 12.55 ($p < .01$) between the C and M groups. The mean death rates during the two heat tests were 1 per cent for litters of the C group, 3 per cent for those of the L group, and 8 per cent for the litters of the M group.

During the heat tests the control rats placed their litters in close piles at places distant from the exposed area, as shown by Figure 7. The *S*s in group L did not gather their litters as well as did the controls, and the litters of rats with median lesions were scattered over the floors of both compartments. The *S*s in groups L and C also constructed nests during the heat tests, as seen by Figure 6, although they had to enter the heated area in order to pick up paper strips. The *S*s with median lesions, however, moved none or only a few strips during these tests.

DISCUSSION

In the present investigation rats which had been subjected to ablations of the median cortical surfaces copulated in a normal manner, gave birth to live pups, and generally severed the umbilical cords and removed the fetal membranes of their young. However, these animals did not gather their litters after parturition and did not permit their young to nurse. They ran aimlessly around in the observation box, frequently picked up and then dropped pups, and rested in places distant from their young. Although they sometimes moved paper strips to one area within a compartment, these rats never constructed nests.

After introduction of foster pups with previous nursing experience, the behavior patterns of these *S*s changed markedly. The foster pups, by hanging on to the nipples of the rats, were able to induce lactation, and the *S*s subsequently hovered over their litters, permitting the pups to nurse. The rats then collected their pups, even after the litters had been scattered, and the foster pups survived. The marked increase in the degree of gathering of the rat's foster litter, as seen in Figure 5, may be an expression of improvement of this aspect of maternal behavior. However, this increase may also be considered as a phenomenon unrelated to maternal behavior. It may be a consequence of the rat's need to suckle its pups in order to relieve the tensions of its swollen mammary glands after the onset of lactation. The independence of lactation and maternal behavior is supported by the findings that, in rats without brain lesions, "destruction of the mammary glands does not abolish or in any way disturb maternal behavior" (4, p. 34).

Maternal activity patterns of rats with lateral cortical ablations of dimensions similar to those of the median ablations (generally less than 25 per cent) were only slightly inferior to those of the control animals. However, lateral ablations of larger dimensions (30 per cent or more) had marked effects on maternal behavior. In the present experiment three rats were used with lateral ablations of 30 per cent, 37 per cent, and 41 per cent (rat no. 51) of the neocortex, respectively, which were not included in group L. These rats exhibited almost total loss of all maternal activity. Although they gave birth to live pups, they only removed the placentae of a portion of their litters, did not gather them, and let them die. They made practically no use of the nesting materials, only occasionally moving a few strips. Foster pups hung on to the nipples of these rats and sucked, but only rat no. 51 was able to lactate, and then only three days after the introduction of the pups, while all the foster pups of the remaining two rats died. Generally, the response of these rats to the air blast and heat tests was to run to a quiet place in the box, stay there, and to ignore their young; only rat no. 51 removed some of its litter from the heated area. The behavior patterns of the two groups of rats with small and large lateral lesions, respectively, are in agreement with those described by Beach (1, 2) and Stone (7).

The limits of the sensory and motor areas of the rat's cerebral cortex were determined by Woolsey by means of electrophysiological techniques. His results are shown diagrammatically by Zubek (10, p. 343), who also designated a "silent" area from which no evoked potentials could be recorded to any type of sensory stimulation, and no motor responses could be observed when this area was stimulated. This silent area is shown as a cortical strip along the mid-line of the brain and seems to be identical with the median cortex. The median cortex includes primarily the cingulate and retrosplenial areas, as designated by Krieg (3), on the basis of histological investigations.

The physiological and behavioral functions of the cingulate cortex have not been investigated extensively in animal or man. In a review of the functions of the "olfactory brain," Pribram and Kruger (5) found evidence for three separate systems in the rhinencephalon. The third system is composed of the cingulate, entorhinal, and retrosplenial cortex and Ammon's formation, whereas the frontotemporal cortex and amygdaloid complex are included in the second system. In an evaluation of investigations on the functions of certain structures in these two systems, Pribram and Kruger came to the conclusion that ". . . at present, an abundance of evidence implicates the second rather than the third system in emotional and social behavior, whereas evidence with respect to the functions of the third system remains sparse . . . up to now there have been no reliable clues from behavioral studies as to the function of the third system" (5, p. 129).

On the basis of the present evidence the third system appears to be involved in hoarding (6) and in maternal activity, which are both relatively complex and well-integrated patterns of unlearned behavior. The third system, or the cingulate cortex, may therefore be implicated in behavior patterns of this kind.

SUMMARY

Three groups of multiparous albino females were used: 11 unoperated rats, 12 *S*s with lesions of the dorsolateral cortical surfaces (the lateral group), and 16 *S*s with lesions of the median cortical surfaces (the median group). The maternal behavior of the *S*s was observed in an observation box, consisting of two compartments with a connecting passage. Strips of paper toweling were scattered on the floor of one compartment. Rating scales were developed for judging the quality of nest construction and the degree of gathering of the rat's litter. The following results were obtained.

1. The mean of the cortical lesions was 17.5 per cent for the lateral and 15.8 per cent for the median group, respectively.

2. The mean size of the litters at birth was 9.0 for the unoperated, 9.8 for the lateral, and 9.3 for the median group, respectively. At the termination of the experiments, on the sixth day *post partum*, the survival of the original litters was 93 per cent for the unoperated rats, 79 per cent for the lateral group, but only 12 per cent for the median group. After foster pups had been placed with *S*s of the latter group, they were able to induce lactation in these rats, and 98 per cent of the pups survived at the end of the experiment.

3. All *S*s in the unoperated and lateral groups began to construct nests with the paper strips several days prior to parturition, and after parturition they built compact nests. Rats with median lesions never constructed nests, but only assembled the strips for loose floor coverings.

4. The control and lateral groups kept their litters close together, hovered over them, and suckled the young. The original litters of the *S*s with median lesions were scattered over the floors of both compartments, and were not nursed. After foster pups had been placed with these *S*s, however, the degree of gathering improved, and on the fourth day *post partum* the litters were gathered nearly as well as those of the other two groups.

5. The nests of the *S*s were destroyed by a strong air blast during hour-long trials on three successive days, starting with the first day *post partum*. Rats in the control and lateral groups rebuilt their nests in a corner of the undisturbed compartment and placed their pups in the new nests during each of these trials. Rats with median lesions did not reconstruct nests and, although they moved a

majority of their litters from the air blast, they did not collect them in one pile.

6. During the succeeding two days the litters were exposed to radiant heat for periods of 1 hr. Rats in all groups moved their young from the heat, but only the control and lateral groups moved paper strips to cover their litters.

During the air blast and heat tests the *S*s of the control and lateral groups moved strips and pups in a rapid and orderly manner, whereas *S*s with median lesions ran aimlessly around the compartments, picking up and dropping pups in all parts of the observation box.

The median cortex consists primarily of the cingulate and retrosplenial areas. Previous investigations found that these structures are not implicated in sensory, motor, or emotional functions. It seems likely that the median cortex has a unique function in the integration of complex unlearned behavior patterns.

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ANALYSIS OF VARIABLES INFLUENCING ALTERNATION AFTER FORCED TRIALS

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Taken at face value, the phenomenon of alternation following forced trials that has been demonstrated by Zeaman and his associates (5, 8, 9) is little short of a catastrophe for S-R learning theory. According to any extant version of S-R theory, the reinforcement of runs to a given side of a T maze should increase the tendency to go to that side, and should yield positive transfer if stimuli are changed. Yet in the studies of Zeaman *et al.* it is regularly found that after a series of forced, reinforced trials to a given side of a T, the rat goes to the opposite side on subsequent test trials. The suggestion of Zeaman that this phenomenon is primarily a manifestation of reactive inhibition does not seem satisfying to us. In the experiments which have provided the empirical basis for the concept of reactive inhibition, activity of the subject (*S*) is severely limited, time intervals between trials are a matter of seconds, and usually large numbers of trials or large work-loads are required to produce substantial decremental effects. But in the forced-trial experiments, the work loads are very small, time intervals between forced trials and test trials range up to 12 hr., and unrestricted activity is permitted during the intervals. It is hardly credible to us that any reasonable concept of work inhibition would account for data obtained under the latter conditions. The issue cannot be settled by argument, however. The phenomenon must be analyzed experimentally in order to isolate the variables upon which the alternation depends and to ascertain whether or not they are response-specific as required by the concept of reactive inhibition. Accordingly, we have undertaken a series of experiments planned, first, to replicate the first part of the Zeaman and House study with some additional controls, and second, to study separately the dependence of the observed alternation upon response variables and upon stimulus variables.

METHOD

Subjects

The *S*s were 14 male and 10 female albino rats, about 240 days old; the males had previously been run in an operant conditioning experiment involving water reinforcement for a tail movement. The total group was subdivided into three groups of males, M1, M2, and M3, with *N*'s of 6, 4, and 4, respectively; and two groups of females, F1 and F2, with *N*'s of 6 and 4, respectively. These designations will be useful in keeping track of the assignments of groups to experiments.

Apparatus

The animals were run on an elevated, single-choice maze, similar to the maze used by Zeaman and House (9) in all respects except that each arm of the T was divided into a 20-in. section adjacent to the choice point and a 10-in. section containing the food receptacle. The maze was centered in a 6-ft. by 8-ft. experimental cubicle and diffusely illuminated by overhead lights located outside the cubicle.

General Procedure

During two days of pretraining the *S*s were handled, and each *S* was given short (ca. 1-min.) periods of access to food on a detached goal stand until it had eaten promptly on two consecutive occasions. The *S*s were run under approximately 23-hr. food deprivation throughout the experiment. On each maze trial (except in Preliminary Experiment [*c*]) *S* was permitted to eat moist Purina mash for 5 sec. on the goal stand; about 20 min. after a group had been run, the animals were given 20 min. access to mash in their living cages.

As in the Zeaman and House study (9), forced trials were accomplished by removing the appropriate sections of the maze, leaving a single pathway from the starting point to the goal stand. Intervals between forced trials were 10 sec., including eating time. In the first part of the first preliminary experiment, the interval from the last forced trial to the test trial also was 10 sec., but after the fourth day this interval had to be increased to 30 sec. in order to allow time for switching maze arms, and remained at 30 sec. throughout the remainder of the study. The directions to which a given *S* was forced on consecutive days were determined by one of the orders LRRLRLLRLR or RLLRLRRLRL; these orders were counterbalanced within groups and repeated as necessary.

A response, left or right, was recorded on a test trial when the animal first placed all four paws on the maze arm to either side of the choice point. Alternation on a test trial will be defined as a left response by a rat which had just received a block of forced trials to the right side of the maze or a right response by a rat which had just received a block of forced trials to the left.

PRELIMINARY STUDIES

Preliminary experimentation was undertaken in order to make sure that the basic findings of Zeaman and House (9) could be replicated and to check on the possibility that the animals were responding to their own olfactory trails.

EXPERIMENT 4

Alternation with Respect to a Randomly Varied Stimulus Characteristic

From the preceding experiments, it would appear that alternation following forced trials does not depend upon reactive inhibition or similar response-associated variables, and must therefore be a function simply of repetitive exposure to particular stimulus conditions. In order to gain more direct evidence concerning the latter aspect of this interpretation, we have conducted an experiment with the situation modified so as to permit repeated exposure of the animal to a particular stimulus characteristic over series of forced trials which involved varied response sequences. The additional apparatus required consisted of two removable covers for the tops of the maze arms. Each of these covers was 20 in. long, with a hardware cloth top 1½ in. wide and sheet metal sides extending approximately 2 in. down the sides of the maze arm; one cover was painted white and the other black. On test trials, in this experiment, the animal was run on a T pattern with both covers in place so that one arm was white and the other black. On forced trials, one arm was removed.

The 16 rats used in this experiment included groups M1 and M2 and three rats each from groups F1 and F2. Each animal was given ten forced trials followed by a test trial on each of six days. Within each block of forced trials, the rat was forced five times to the left and five times to the right in one of the two orders that had been used for assigning sides in previous experiments. (Cf. General Procedure above.) By appropriate placement of the covers, the animal was forced to go uniformly either to a black or to a white arm on all ten of the forced trials in a block, then given a choice between a black and a white arm on the test trial. Over the first two days, each rat was forced to white on one series and to black on one series, with the same order of left and right forced trials on both days and the same left-right positioning of the black and white maze arms on both test trials. Over the last four days, each rat was forced uniformly to the color that it had been forced to on the first day (i.e., white in half the cases and black in half); the two orders of left and right forced trials and the left-right positions of the black and white maze arms were alternated from day to day.

For purposes of analyzing the data of this experiment, alternation will be defined as choice on a test trial of the white maze arm if the preceding forced trials had been to black or choice of the black arm if the forced trials had been to white. Percentages of alternation, so defined, on the six test trials were 56, 62, 69, 69, 69, and 62, respectively. Mean frequency of alternation over the six days differed from chance at the .01 level (t of 3.18 with 15 df), and the mean over the last four days only differed from chance at the .05 level (t of 2.31 with 15 df). The confidence levels were unchanged when the data were subjected to an arcsine transformation (t values of 2.95 and 2.70, respectively, on the transformed scores). It may be noted that the test trial data do not deviate significantly from chance expectation in any other respect that we have been able to detect. There is a slight over-all bias in the direction of right turns, but the difference between the obtained mean of 56 per cent right turns and the chance value of 50 per cent is not significant at the .05 level. If alternation is defined with respect to the direction of the last forced run preceding the test trial, an over-all mean of only 52 per cent alternation is obtained. Apparently we may consider that the only systematic relationship manifested in these data is that of alternation with respect to color.

GENERAL DISCUSSION

The findings of this series of experiments indicate that alternation after forced trials is best described in terms of a tendency to approach "new" rather than "old" stimuli. By "old" and "new," we refer of course to stimulus variables associated with areas which the animal has or has not, respectively, traversed during the forced trials. Our conclusion is somewhat at variance with that of Zeaman and his associates (5, 8, 9), who concede that "place alternation" does occur, but still find a place for reactive inhibition in their account of the phenomena. It may be noted, however, that in their entire series of studies there is only one observation which can be interpreted as pointing directly to a dependence of the alternation upon response-associated variables. This observation comes from Experiment 4 of the Rothkopf and Zeaman study (5), which is similar to Experiment 2 of the present study in all respects except that in their experiment the orientation of the maze in the room was changed by 180° between the forced and test trials while in ours the orientation was changed only 90°. The difference in results, 69 per cent "response alternation" after ten forced trials in their study and only 50 per cent in ours, is not easy to account for. If Rothkopf and Zeaman's interpretation in terms of reactive inhibition were correct, then our experiment should have yielded more, rather than less, "response alternation," since in their study, if place and response alternation tendencies, both exist, must have been directly opposed, while in our study only response alternation could have been operative.

Even if it is granted that the animal can discriminate stimuli that have recently been approached from those that have not, the question remains why it tends to avoid the former on free-choice trials. The type of explanation favored by most recent investigators involves positing an attribute or characteristic of the animal which has the necessary properties to account for the phenomena. The concept of "exploratory tendency" proposed by Montgomery (4), that of "stimulus satiation" proposed by Glanzer (2), and that of "tired stimuli and tired responses" proposed by Zeaman (5, 8) all fall in this category. For our part, we are inclined to postpone consideration of any of these explanations which necessitate endowing the animal with hypothetical processes or mechanisms of great generality until more parsimonious alternatives have been systematically excluded. In the latter category, one rather simple possibility is that the alternation represents transfer from learning which has occurred either during pretraining or in the extra-laboratory environment prior to the experiment. There would be a basis for this transfer if there were in normal environments a negative correlation between probability of receiving reinforcement in a given location and recency with which the location has been visited. What the average value of this correlation may be under ordinary living conditions in an animal colony is a matter of sheer conjecture. However, it should not be difficult to modify the correlation experimentally.[1] Further, it seems fairly obvious that on any given run during maze training, the animal is differentially reinforced for approaching "new" stimuli and nonreinforced for retracing, i.e., approaching "old" stimuli. Unless possibilities of this sort can be ruled out, we believe that the data of experiments on alternation should not be assumed to constitute evidence for any type of general decremental factor.

SUMMARY

In the series of experiments reported we have attempted to isolate the class of experimental variables responsible for alternation following forced trials in the T maze. The basic design consisted in giving blocks of massed, forced trials to groups of rats, then giving alternation tests under appropriate conditions. The principal findings were as follows:

1. The phenomenon of alternation following massed, forced runs to one side of a T maze, originally reported by Zeaman and House, was replicated with experimentally naive rats; controls showed that the animals were not responding to their own olfactory trails.

2. Forced runs to one side of the maze over a pathway which required both a left and a right turn on each trial were followed by nearly 100 per cent alternation.

3. When forced runs to one side of the T pattern were followed by tests with the orientation of the maze in the room changed by 90°, alternation dropped to a chance level.

4. During a series of test trials, the alternation tendency produced by preceding forced runs extinguished rapidly to a chance level.

5. Forcing animals repeatedly to a black or a white maze arm which varied in left-right location from trial to trial resulted in significant alternation with respect to the black-white stimulus variable.

It was concluded that alternation following forced trials does not depend upon response-associated variables, but is a function of repetitive exposure to particular stimulus conditions. Consequently, an interpretation in terms of reactive inhibition seems untenable. It was suggested that alternation may represent a transfer phenomenon rather than a manifestation of a general decremental process.

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[1] A fragment of relevant evidence is available from an experiment conducted by John Grossberg and Harold Sprinzen in the senior author's advanced laboratory course. Two groups of nine rats were given differential preliminary training for two weeks prior to alternation tests. During the preliminary training, all the animals were permitted, singly, to explore a table top on which food pellets had been placed. For one group, conditions were arranged so that the animals had to avoid approaching recently visited locations in order to obtain pellets, while for the other group, pellets were always available in previously visited locations. When tested subsequently on a Y maze, the first group exhibited significantly (.05 level) more spontaneous alternation.

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THE RESISTANCE TO EXTINCTION OF RESPONSES ACQUIRED UNDER IRREGULAR CONDITIONS OF LEARNING[1]

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This paper reports an experiment designed to investigate whether or not responses acquired under irregular conditions of acquisition are more resistant to extinction than responses acquired under regular acquisition conditions. McClelland (2) points out that a major paradox in learning theory is the fact that laboratory learning is much less resistant to change than learning which occurs under ordinary conditions. He suggests that the discrepancy arises because few laboratory experiments are sufficiently "messy" or disorderly to make the discrimination between learning conditions and extinction conditions difficult enough for the organism. In the laboratory regular relationships hold within the cue-reward-response sequence, whereas under ordinary circumstances learning must often occur under irregular, changing, and inconsistent conditions.

To date, the only experimental investigation of the relationship between irregularity of acquisition conditions and resistance to extinction was conducted by McClelland and McGowan (3). Although their experiment provided evidence supporting McClelland's suggestion, the experimental design did not provide for the partialing out of the particular influence of each of the separate variables.

On the basis of McClelland's suggestion, an experiment was conducted to test the general hypothesis that the more irregular the conditions of acquisition of instrumental responses, the greater the resistance to extinction of these responses. Three sources of irregularity were introduced into the acquisition conditions: (*a*) differing reinforcement schedules (total versus partial reinforcement), (*b*) differing numbers of manipulanda (one versus two versus three), and (*c*) differing drive-reduction conditions (hunger versus hunger or thirst on a given trial).

This choice of sources of irregularity made it possible to state three specific testable hypotheses. The test of the specific hypotheses required that (*a*) the total number of reinforcements during acquisition be held constant for all groups, and (*b*) the number of hours of food and water deprivation during acquisition and extinction be held constant.

The specific hypotheses are:

1. The more irregular the conditions of reinforcement of instrumental responses during acquisition, the greater will be the resistance to extinction.
2. The greater the number of types of responses which during acquisition have been instrumental in obtaining primary reinforcement, the greater will be the resistance to extinction.
3. The greater the number of primary drives reduced by instrumental responses during acquisition, the greater will be the resistance to extinction.

EXPERIMENTAL DESIGN

Sources of Irregularity

Table 1 presents in detail the sources and variations of irregularity of acquisition conditions. Also, the table provides a reference for the symbols used hereafter in designating the various groups, each one of which represents one variation within each of the three sources. The assumption was made that A1 represented less irregularity than A2, B1 less than B2, B2 less than B3, and C1 less than C2. Positive reinforcement was defined as remaining in the goal box on one occasion for 20 sec. in the presence of available food or water. Zero reinforcement was defined as the removal of the rat from the response box to its home cage immediately after the response appropriate for that trial was made; consequently, on zero reinforcement trials the rat was not allowed to enter the goal box nor was the goal box door opened. For the A2 groups the order of positive and zero reinforcement trials was randomly predetermined. Only one manipulandum was "appropriate" for any given trial, that is, a response on only one manipulandum was instrumental either in opening the door to the goal box, or led to the removal of the rat to its home cage. For groups which were trained on more than one manipulandum (B2 and B3), the one designated to operate on each trial was randomly predetermined. Although both hunger and thirst drives were always present, only one type of primary reward was given on each trial, and presumably one or the other of hunger or thirst was reduced. For the C2 groups the order of presentation of primary rewards was randomly predetermined.

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[1] This report is part of a dissertation submitted in June, 1954, to the Department of Psychology at the University of Nebraska in partial fulfillment of the requirements for a Ph.D. degree. The writer wishes to express appreciation to Dr. W. J. Arnold, who supervised the research, and to Dr. K. E. Baker for additional guidance.

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Combination of Sources of Irregularity

The sources of irregularity and variations of irregularity within each source were combined in a 3 × 2 × 2 factorial design, which allowed for the systematic combination of the conditions of irregularity in 12 different ways. One variation of each of the sources of irregularity was represented in the acquisition conditions of each group. Group A1B1C1 was trained under the most regular conditions. For this group pulling the chain was instrumental in the attainment of food on 100 per cent of the trials. For Group A2B3C2, trained under the most irregular conditions, one or the other of the responses of pulling the chain, pressing the horizontal bar, or pushing the vertical bar was instrumental in the attainment of either food or water on 80 per cent of the acquisition trials.

The systematic combination of the sources of irregularity provides a measure of the interaction effects between the three sources of irregularity, a type of empirical information which has been totally neglected in investigations of extinction. The experimental design also approximates the requirements demanded by Brunswik (1), in that it studies behavior under conditions which, because of the concomitant variation of several variables, at least approach representativeness of actual life conditions.

Extinction Criteria

Two criteria of extinction were used, one to parallel common practice, and the other to provide a more complete measure. Criterion I was four successive 2-min. trials with no responses on appropriate manipulanda. This criterion was as stringently or more stringently defined than the usual criterion for extinction. Criterion II, employed for the purpose of including spontaneous recovery aspects of the extinction process, was eight successive 2-min. no-response trials, four on one day and four on the next day. Criterion II is more stringent than merely reaching criterion I on two occasions, since it allows ample opportunity for the reaction tendency to rise above the reaction threshold because of the dissipation of inhibitory potential. Criterion I may be reached upon several occasions before criterion II is met. Each of these occasions indicates that reaction tendency has been lowered but only to an extent which is insufficient to counteract the opposing spontaneous recovery. The greater the number of these occasions, the more criterion II seems to be measuring a different aspect of the extinction process as a whole.

The use of two extinction criteria is important for several reasons. First, it is conceivable that the interpretation of an investigation may vary with the manner in which extinction is defined. Secondly, as Underwood (4, p. 45) points out, there is need for more empirical information concerning spontaneous recovery. Thirdly, for those interested in the practical problems of extinction, it is of interest whether or not a response has been completely extinguished rather than temporarily depressed, as is indicated with the use of a criterion like our

TABLE 1

Sources and Variations of Irregularity of Acquisition Conditions

Source	Variation
A. Reinforcement schedules	A1. 100% positive reinforcement A2. 80% positive and 20% zero reinforcement
B. Number of manipulanda	B1. Chain B2. Chain and horizontal bar B3. Chain, horizontal bar, and vertical bar
C. Number of drives reduced	C1. Hunger C2. Hunger and thirst

criterion I. Finally, to study the effects of irregularity in the spontaneous recovery process itself, it is necessary to use the two criteria for comparison purposes.

METHOD

Subjects and Apparatus

The *S*s were 48 naive rats, ranging in age from 120 to 180 days at the beginning of training. Two male and two female rats were assigned to each of 12 groups on the basis of age and litter.

Figure 1 presents a diagram of the apparatus employed in the experiment. The apparatus consisted of a box 48 by 16 in., which was divided by vertical sliding doors into three compartments, the starting box, the response box, and the goal box. The response box contained three manipulanda, a chain, a horizontal bar, and a vertical bar which, when operated under the appropriate circumstances, caused the door to the goal box to open. When this door opened, the rat could pass along a short runway to enter the goal box, where food (wet mash) or water was placed. Three selector switches enabled *E* to determine which manipulandum, when operated, would open the door. A by-pass switch allowed *E* to open the goal box door without any one of the manipulanda being operated, and another switch prevented the opening of the goal box door when the selected manipulanda were operated. The *E* manually reset the door to its closed position.

The electrical wiring of the apparatus permitted the automatic recording of response characteristics. A direct record of all appropriate responses (that is, responses made on manipulanda whose selector switches were "on") appeared on an electric counter even when the door to the goal box was prevented from opening. Furthermore, each response made on any manipulandum, no matter whether or not that manipulandum was "on," was recorded on polygraph tape. For both acquisition and extinction, the polygraph tape provided a permanent record of the total number of responses in a trial, the number of responses made on each manipulandum, order of use of manipulanda, and the latency of all responses.

Procedure

Groups of four rats were handled as a unit during the experimental session. Throughout the entire experiment the trials were spaced, that is, rat 1 was given trial 1, rat 2 trial 1 . . . rat 4 trial 1, then rat 1 was given trial 2. After the first day of preliminary training the *S*s were under approximately 21.5-hr. food and water deprivation at the beginning of each experimental session.

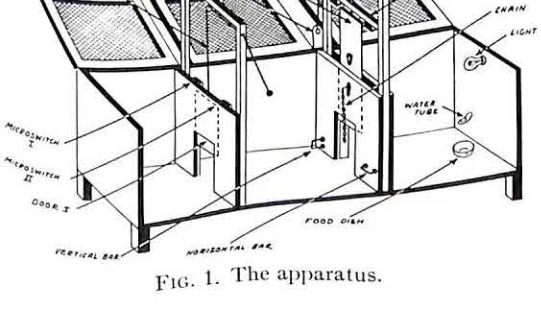

FIG. 1. The apparatus.

Preliminary Training

Preliminary training consisted of training the rats to run from the starting box to the goal box when the doors were opened by *E*. This training was identical for all groups, except that for the C2 groups either food or water, and for the C1 groups, only food was placed in the goal box. Preliminary training lasted four days.

Acquisition Training

For all groups acquisition training began the day after preliminary training ceased, and lasted seven days. All manipulanda were uncovered for all trials but only one manipulandum was "on"; consequently, a response had to be made on the manipulandum which was "on" in order to open the door to the goal box (or to be removed to the home cage on zero reinforcement trials). Groups trained under condition A1 were given the same number of reinforced trials per day as groups trained under condition A2. However, for the A2 groups additional zero reinforcement trials were included so that these groups completed a total of 112 trials in the same number of days required for the A1 groups to complete a total of 90 trials. The zero reinforcement trials were interspersed among the reinforced trials; an equal number of responses on each appropriate manipulandum received zero reinforcement.

On a typical acquisition trial, the rat was placed in the starting box, and the door from the starting box was opened. When the response appropriate for that trial was made, the door to the goal box opened. The rat entered the goal box and remained in it for 20 sec. On zero reinforcement trials, as soon as the rat made the appropriate response, it was removed from the response box to its home cage. After the completion of the required number of trials for the day, food and water were placed in the home cages for 10 min.

Extinction Training

Extinction training began the day after acquisition training was completed. The extinction procedure was identical for all rats in all groups. Each rat was given ten, 2-min. spaced extinction trials per day. The interval between the trials for each rat was approximately 10 min. Two minutes after the starting box door opened, the rat was removed to its home cage. After the completion of ten trials, food and water were placed in the home cage for 25 min.

Throughout extinction the door to the goal box never opened. All manipulanda were uncovered, and for each group all manipulanda which had been appropriate for that group during acquisition were "on" for all trials. Consequently, all responses on appropriate manipulanda were recorded on the counter; all responses whether on appropriate manipulanda or not, were recorded on the polygraph tape.

Extinction training was continued in ten-trial daily sessions until criterion I (four consecutive 2-min. trials with no responses on appropriate manipulanda) was reached. When a rat reached criterion I, it was given no more trials on that day. However, on the next day, and all days thereafter *S* was given the usual extinction training until criterion II (eight successive no-response trials, four on one day and four on the next day) was reached. For the purposes of this investigation, when criterion II was reached, extinction was considered complete, and the rat was dropped from the study.

RESULTS

Criterion II Data

Table 2 presents the means, standard deviations, and variances of log responses to criterion II for each of the 12 groups of rats. Each group was trained under different conditions of irregularity during acquisition. Analysis of variance was applied to this data and also to the corresponding data for log trials to criterion II. The analyses of variance indicate that for both indices of extinction the differences between number of manipulanda are significant beyond .01 level. The differences between reinforcement schedules for both indices are significant beyond the .05 level. For neither type of data is the difference between drive reduction conditions significant. All significant differences are in the predicted direction. None of the interaction effects is significant.

To summarize, the statistical analysis of log trials and log responses to criterion II provide support for the general hypothesis that the more irregular the conditions of acquisition, the greater the resistance to extinction. Furthermore, the analyses provide definite evidence in support of the first two specific hypotheses. The A2 groups (partial reinforcement) made more responses and required more trials to reach criterion II than did A1 groups (total reinforcement). The B3 groups (three manipulanda) required more trials and made more responses than did B2 groups (two manipulanda), while B2 groups showed more resistance to extinction than B1 groups (one manipulandum). The third specific hypothesis is not supported since C2 groups (reduction of two primary drives) did not show more resistance to extinction than C1 groups (reduction of one primary drive).

TABLE 2

Means, Standard Deviations, and Variances of Log Responses to Criterion II

	A1 Total Reinf.	A2 Partial Reinf.	A1 Total Reinf.	A2 Partial Reinf.	Total
B1—One manip.					
Mean	2.05	2.44	2.35	2.44	2.32
SD	.17	.24	.11	.28	.26
Var.	.04	.08	.02	.10	.07
B2—Two manip.					
Mean	2.65	2.90	2.70	2.74	2.75
SD	.18	.15	.25	.17	.21
Var.	.04	.03	.08	.04	.05
B3—Three manip.					
Mean	2.92	3.06	2.86	2.92	2.94
SD	.32	.12	.48	.14	.31
Var.	.14	.02	.30	.03	.10

Totals for A and C Conditions

	A1 Total Reinf.	A2 Partial Reinf.	C1 One Drive Reduced	C2 Two Drives Reduced
Mean	2.59	2.75	2.67	2.67
SD	.41	.31	.40	.34
Var.	.18	.10	.17	.12

Criterion I Data

Analysis of variance was also applied to log trials and to log responses to criterion I. For both types of scores the differences between manipulanda conditions are significant beyond the .01 level. For neither log responses nor log trials is the difference between reinforcement schedules significant. However, for both types of scores, the differences which do exist between the total and partial reinforcement conditions are in the predicted direction. The difference between number of drives reduced is not significant for both log trials and log responses to criterion I, and the differences which did occur are not in the predicted direction. For both log trials and log responses the interaction effects between reinforcement schedules and number of drives reduced (A × C) are significant beyond the .05 level.

The analyses of log trials and log responses to criterion I definitely substantiate specific hypothesis 2, provide evidence in favor of specific hypothesis 1, and do not support specific hypothesis 3. Some fairly strong support is given to the general hypothesis, but this support is not so clear-cut as that supplied by the criterion II data. The Pearson *r*'s of .90 and .91 between log trials and log responses to criterion II and criterion I, respectively, indi-

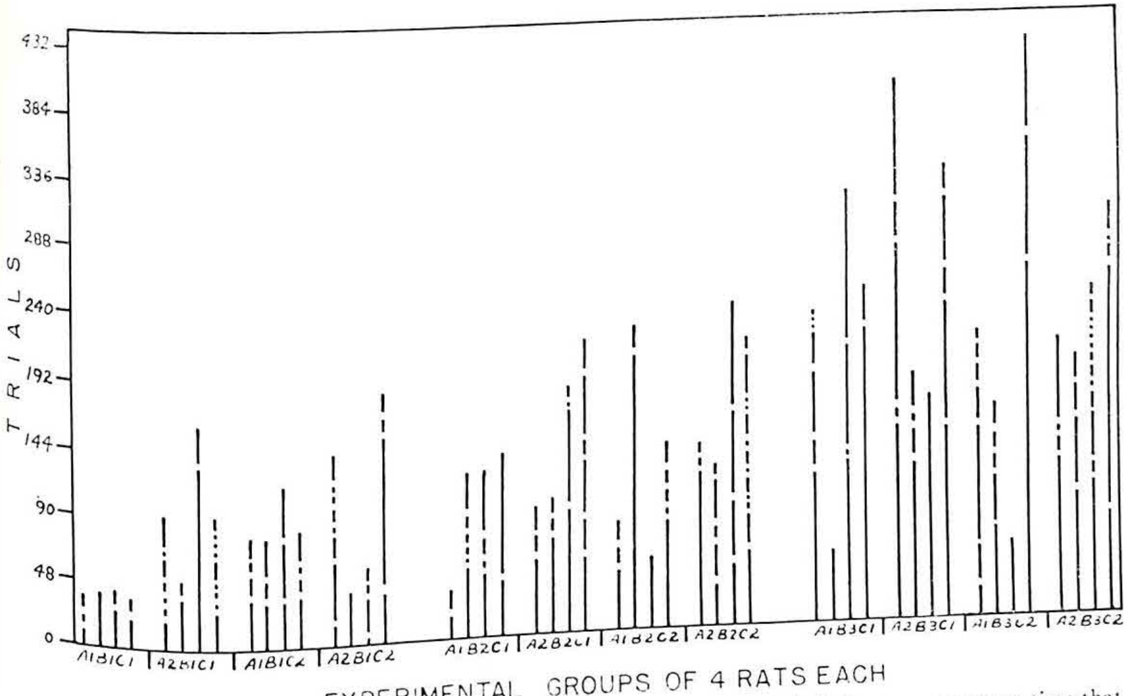

FIG. 2. Number of trials to criterion II for each of 48 rats. Each gap in the black line represents one time that criterion I was reached, and the interval between the gaps represents the number of trials between successive times that criterion I was reached.

cate that the two indices of resistance to extinction are closely related.

Correlation between Criterion I and Criterion II Data

Certain relationships between irregularity of acquisition conditions and resistance to extinction varied with the criterion of extinction. As one measure of the extent of the relationship and differences between the two sets of data, Pearson r's were calculated. The r's of .69 between log trials and .87 between log responses to criterion I and criterion II indicate a definite relationship between the two criteria. However, the r's are deceptively high because the scores to criterion I are included in the scores to criterion II. Obviously, much of the variance for log scores to one criterion could not have been predicted on the basis of log scores to the other criterion, and, therefore, the two criteria must measure somewhat different aspects of the extinction process.

Spontaneous Recovery Data

A further analysis was made on the differences between the two criteria by considering the number of occasions that spontaneous recovery occurred. Because of the definition of criterion II, it was possible for a rat to reach criterion I several times before criterion II was attained. By definition, spontaneous recovery occurred if responses were made after criterion I had been reached. Some rats made responses for several days before criterion I was reached for the second time. The interval between each successive occasion that criterion I was met, is referred to as one occasion during which spontaneous recovery occurred, provided that some responses were made during this interval.

Figure 2 shows the number of times that each rat reached criterion I, and the number of trials that intervened between successive occasions that criterion I was reached. The over-all trend indicates that the greater the irregularity of acquisition conditions, the more frequently spontaneous recovery occurred. The analysis of variance, applied to the number of occasions that spontaneous recovery occurred, indicates that the difference between reinforcement schedules is significant beyond the .05 level. Spontaneous recovery occurred on more occasions for A2 groups (partial reinforcement) than for A1 groups (total reinforcement). Thus, when the index of resistance to extinction is the number of occasions that spontaneous recovery occurs, there is some support for the hypothesis that responses acquired under irregular conditions tend to be more resistant to extinction. Figure 2 also indicates that the number of trials between successive attainments of criterion I does not always become progressively less. Since the number of trials and responses are highly correlated, it would seem that extinction is not necessarily a gradual and progressive decline in response strength. Thus, Figure 2 provides substantiating evidence for the contention that acceptance or rejection of hypotheses may depend upon the definition of the extinction criterion.

DISCUSSION

On the basis of this experiment it seems reasonable to conclude that for at least some sources of irregularity, the more irregular the conditions of acquisition the greater the resistance to extinction. The sources of irregularity which have been shown to affect resistance to extinction are differing reinforcement schedules and differing numbers of manipulanda. Consequently, specific hypothesis 1 and specific hypothesis 2 are supported. This differential resistance to extinction was demonstrated when extinction was measured to a rigorous criterion which included measurement of behavior which, according to the more usual extinction criteria such as criterion I, would be called spontaneous recovery. Furthermore, the conclusion that resistance to extinction may depend on irregularity of acquisition conditions, is based on two indices of extinction, trials to criterion and responses to criterion. Specific hypothesis 3 concerning irregularity in the number of drives reduced was not supported; however, the acceptance of the null hypothesis does not seem justified for reasons to be discussed later.

The conclusions would have been somewhat different had the less stringent criterion I alone been used. For example, although the conclusions concerning specific hypotheses 2 and 3 are the same for both criteria, this is not true for specific hypothesis 1. Furthermore, interaction effects between reinforcement schedules and drive reduction conditions were significant when criterion I was used, but not when criterion II was used. These discrepancies would seem to call for further investigation.

It is not surprising that the conclusions based on the two criteria differ somewhat, since criterion II included measurement of spontaneous recovery. Although it would seem that the entire phenomenon of spontaneous recovery requires investigation, this study permits the conclusion that an extinction criterion which includes spontaneous recovery measures an aspect of the extinction process different from that which is measured by a less stringent criterion. Consequently, caution is required when comparisons are made between sets of empirical data, if the extinction criteria have not been defined identically.

The only interaction effects found to be significant were between reinforcement schedules and drive reduction conditions when criterion I was used. Therefore, in this experiment the conclusions would not have differed greatly had the variables not been combined. Since the interaction effects to criterion II were not significant, it seems safe enough to expect that differing reinforcement schedules and differing numbers of manipulanda would affect resistance to extinction even if these variables were not combined. It seems that the combination of these sources of irregularity neither adds more nor less resistance to extinction than would the two variables when considered separately.

These results provide evidence in favor of McClelland's general prediction that the more disorderly and confused the original conditions of acquisition, the harder it is to set up conditions which are sufficiently different from them for the organism to perceive the difference and unlearn a response which is no longer appropriate. Although our results do not warrant the conclusion that all types of irregularity in acquisition conditions affect resistance to extinction, we have shown that for at least two types of irregularity, the relationship suggested by McClelland does hold. McClelland's suggestion pertained to learned motives while this investigation was of learned instrumental responses. In as far as the same learning process is involved in acquiring motives and instrumental responses, these results may be taken as an indication that irregularity of acquisition conditions also affects the persistence of learned motives. However, the conclusions are applicable to human learning only in so far as it is reasonable to generalize from rat learning to human learning.

McClelland (2), in his discussion, points out that in ordinary learning situations sometimes a response is reinforced, and sometimes the same response is not reinforced, or may even be punished. In an attempt to duplicate ordinary learning conditions, the experiment was designed specifically to allow groups B2 and B3 to make responses which would not be reinforced. Because of this it is possible that, although each group received the same number of reinforcements, the learning which took place in condition B3 may have differed from that of B2, which in turn, may have differed from that of B1. That is, the *S*s in B3 groups made more responses per trial (operated more manipulanda on the average) in order to obtain reinforcement than the *S*s in B2 or B1. It would perhaps follow that since the B3 groups made more responses during acquisition, response strength for those groups should be higher at the completion of acquisition training. Because of this higher response strength, the B3 groups would then be expected to make the more responses during extinction. However, many of the responses made by the B3 groups during acquisition were not reinforced, and it is likewise probable that because of the nonreinforcement, inhibitory potential was generated, and response strength was lowered. If the latency of the first response is taken as a measure of response strength, then it would seem that the response strength of the B3 groups was actually lower at the end of acquisition training than the response strength of the B2 and B1 groups. The mean latency for the first response for the last ten acquisition trials for groups B3, B2, and B1 were 10.9, 4.7, and 3.1 sec., respectively. Obviously, it cannot be stated unequivocally that response strength for the three groups was equal at the termination of acquisition training, nor, if it was unequal, which group had the greatest response strength. However, the test of the hypotheses does not demand that all groups have equal response strength at the end of the acquisition training. If response strength were equal for all groups, it is unlikely that resistance to extinction would vary. Variation in the number of responses made during acquisition was required as a test of the influence of this particular source of irregularity upon resistance to extinction.

A word of caution should be given concerning the conclusions based on the results of this experiment. While it has been shown that the relationship between irregularity of acquisition conditions and resistance to extinction does seem to hold for this particular reinforcement schedule and for these numbers of manipulanda, there is no reason to believe that the relationship would hold throughout the entire continuum of irregularity. Moreover, although we have shown that up to three manipulanda, the addition of one manipulandum does add an increment in resistance to extinction, it is conceivable that after a point, the addition of one manipulandum would not appreciably affect resistance to extinction.

Although we were unsuccessful in demonstrating a difference between the number of drives reduced (hypothesis 3), acceptance of the null hypothesis may not be justified. The negative results may have been due to the fact that the food reward was wet mash. Consequently, on trials in which food reward was given, it is possible that both the hunger and thirst drives were reduced. Because of this, there was perhaps little difference in drive reduction for the C1 and C2 groups. An unequivocal answer to this question awaits further research in which more care is taken to control the drive reduction conditions.

The findings of the present study are encouraging in that they provide some information which may be accepted as a partial explanation of the differential resistance to extinction between laboratory and natural-life learning. The positive results make it specially pertinent that other sources of irregularity, not sampled here, be investigated in further studies. The investigation of this concept in relation to learned drives and acquired motives would seem particularly desirable.

SUMMARY

An experiment was conducted to test the general hypothesis that the more irregular the conditions of acquisition of instrumental responses, the greater the resistance to extinction of these responses. Three sources of irregularity were introduced into the acquisition con-

ditions: (*a*) differing reinforcement schedules, (*b*) differing numbers of manipulanda upon which instrumental reward responses could be made, and (*c*) differing drive reduction conditions. The sources of irregularity were combined in a 3 × 2 × 2 factorial design so that the influence of each separate source of irregularity upon resistance to extinction and their interaction effects could be measured. Forty-eight rats were assigned to 12 groups of four rats each. During acquisition one variation of each of the three sources of irregularity was represented in each group. The number of positive reinforcements and the hours of deprivation were held constant for all groups.

Following the varied acquisition training, all rats were treated alike during extinction. Two measures of extinction, number of trials to criterion, and number of responses to criterion, were utilized. Resistance to extinction was measured to two different criteria. Criterion I, similar to the usual extinction, was four consecutive 2-min. trials with no responses. Criterion II was eight consecutive 2-min. no-response trials, four on one day and four on the next day. The more rigorous criterion II provided a more complete measure of extinction since it included measurement of spontaneous recovery.

1. For at least some sources of irregularity, the more irregular the conditions of acquisition, the greater the resistance to extinction. Irregularity in reinforcement conditions and in manipulanda conditions caused significantly greater resistance to extinction. Irregularity in drive reduction conditions did not affect resistance to extinction.

2. The measured interaction effects were not significant so that the observed relationship should hold regardless of whether these sources of irregularity are combined or act separately.

3. The number of trials and number of responses to the extinction criteria are highly correlated.

4. Observed differences between the two criteria indicate that a rigorous extinction criterion may measure an aspect of the extinction process different from and in addition to that which is measured by a less stringent criterion. Therefore, caution is needed in comparing the results of experiments if the extinction criteria have been defined differently.

5. The fact that spontaneous recovery occurred on significantly more occasions when rats were trained under partial reinforcement requires further investigation, as does the general relationship between spontaneous recovery and irregularity of acquisition conditions.

6. Data presented show that extinction does not necessarily take place more rapidly as a function of previous extinctions.

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DISCRIMINATION LEARNING AS A FUNCTION OF THE RATIO OF NONREINFORCED TO REINFORCED TRIALS[1]

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Several investigations (1, 2, 6) have indicated the utility of nonreinforced incorrect responses in the learning of a discrimination problem. Fitzwater (1) gave albino rats 40 forced trials on a form discrimination problem under four ratios of nonreinforced trials to reinforced trials, where approaching the incorrect stimulus was always nonreinforced and approaching the correct stimulus was always reinforced. He then recorded the number of correct choices the animals made on each of six consecutive free-choice training days. The results of this study indicated that ratios of incorrect to correct forced choices of 35/5, 30/10, and 20/20 resulted in better performance on the first free day, 16 trials, than the ratio 0/40 involving no nonreinforced forced trials to the incorrect stimulus. No differential effect was found, however, between those ratios which included nonreinforced trials to the incorrect cue.

Any theory which postulates a monotonically increasing curvilinear function for the acquisition of approaching and not-approaching tendencies would predict differences in performance for different ratios. Under this postulate a forced negative trial would be of greater or less advantage than a forced positive trial depending upon the absolute strength of the two tendencies. Two possibilities come to mind to account for Fitzwater's failure to find a difference: (*a*) with his limited set of ratios, none of which involved more positive than negative trials, the differences may have been too small to appear, and (*b*) the animals may not have received the relevant stimulation on each forced trial.

The present study attempts to take into consideration these possibilities by making a different selection of ratios, varying the amounts of forced training, and employing a simple black-white discrimination problem. By recording latency of response to the positive and negative cue during forced training and per cent correct choice on the first free-choice day, two experimentally independent estimates of differential effective excitatory strength (Diff. ${}_{S}\bar{E}_{R}$) to the two cues may be obtained by utilizing the Hullian assumptions relating latency and per cent choice of response to ${}_{S}\bar{E}_{R}$ (3, 5).

METHOD

Subjects

Eighty-four naive rats, 42 males and 42 females, from the laboratory maintained by the Department of Psychology at the University of Michigan were divided into 16 groups, 12 of 6 animals each, and 4 of 3 animals each. Each group contained approximately equal numbers of males and females. The age of the animals ranged from 90 to 120 days at the beginning of training.

Apparatus

The two-choice discrimination box designed by Lawrence (4) for simultaneous discrimination learning was employed. The animal was placed in the starting box, and a guillotine door was lowered, which started a Standard Electric Clock and presented the stimuli to the animal. The two walls and the floor of a goal chamber were made flat black or flat white by arrangement of the metal liners and metal floor. A food cup, attached to and painted the same as the liner, was at the end of each of the 13-in. chambers.

On forced trials one of the chambers was blocked by a piece of metal fitted to the opening and painted a flat gray to match the apparatus. A 2-in. gap separated the starting box from the goal chambers. The guillotine door was raised, stopping the clock, when the animal's hind feet were in the chosen goal chamber.

Procedure

The animals were handled individually and allowed to cross between chairs until they would cross a 4-in. gap and eat pellets from a dish at least three times in a 2-min. period. This preliminary training required approximately 10 to 14 days. The animals were kept in individual living cages and were fed either 8 gm. (males) or 6 gm. (females) of Miller's Homogenized Dog Food daily. Deprivation time was approximately 22 hr.

Forced-trial training. Four ratios of nonreinforced trials to reinforced trials, 0/16, 4/12, 8/8, and 12/4, were combined with ½, 1, 3, and 5 days of forced-trial

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running to form a 16-cell factorial design. The 12 cells employing ½, 1, and 3 days' forced training contain six animals each while the 4 cells for 5 days of forcing contain three animals each. For one-half the animals black was positive, and for one-half white was positive.

One day's running consisted of 16 trials under the appropriate ratio with one-half the positive and one-half the negative trials forced to each side according to a schedule which presented no more than two successive reinforced or nonreinforced trials to the same side. On a positive trial the animal was allowed to eat a moistened pellet of approximately .07 gm. in the presence of the correct cue. On a negative trial the animal was detained a comparable length of time, about 20 sec., in the negative chamber. Trials were spaced by running each of two animals on a given trial before proceeding to the next trial. If an animal failed to cross the gap within 5 min., it was gently pushed out by moving the back wall of the starting box forward.

Free-choice training. On the day following the last forced day and on all subsequent days until the criterion of one perfect day was reached, the animals were presented with 16 free-choice trials with both the positive and negative cue present on each trial. The position of the positive cue was alternated from side to side over trials under the restriction that it appear on each side 8 of the 16 trials each day. No animal was ever pushed on a free-choice trial. The noncorrection procedure was employed.

RESULTS

Both the latency data from the forced trials and the choice data from the free trials were transformed to estimates of Diff. $_{S}\bar{E}_{R}$ according to the Hullian assumptions for analysis purposes.

Hull (3) specifies differential response speed (reciprocal latency) to the positive and negative cue to be linearly related to Diff. $_{S}\bar{E}_{R}$. Figure 1 shows the mean difference in response speed, and hence in $_{S}\bar{E}_{R}$, at the end of forced training for the ratio groups 4/12, 8/8, and 12/4 over ½, 1, 3, and 5 forced days. The overall rank order of the ratio groups from greatest to least difference is 8/8, 4/12, and 12/4. In obtaining each point the reciprocal of the median latency of approach to the negative cue for each animal on the last forced trial to the right and to the left was subtracted from the corresponding response speed for the positive cue. The points for ½, 1, and 3 forced days are each based upon six animals while the points for 5 forced days involve three animals each. The analysis of variance for the two-dimensional factorial design is summarized in Table 1, where it may be seen that the three ratio groups which involve trials to the negative cue differ in Diff. $_{S}\bar{E}_{R}$ ($p < .05$). Figure 1 indicates that it is forced days 1, 3, and 5 which yield this result. The main effect for Days Forced is highly significant ($p < .001$) while the F for

TABLE 1

Analysis of Variance of Differences in Response Speed at the End of Forced Training

Source	*df*	Mean Square	*F*
Days	3	0.8531	26.865
Ratios	2	0.1077	3.387
D × R	6	0.0336	
Within cells	51	0.0318	
Total	62		

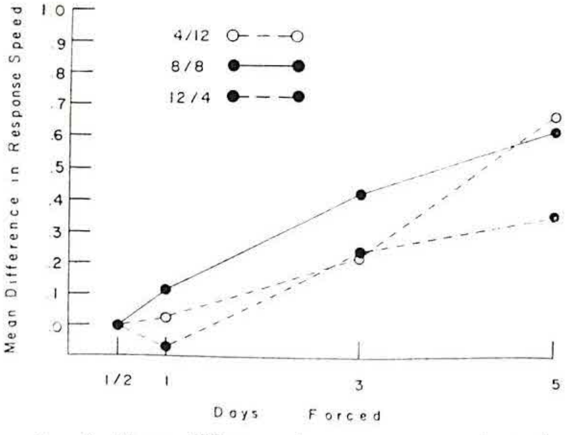

FIG. 1. Mean difference in response speed at the end of forced training for the ratio groups 4/12, 8/8, and 12/4 over ½, 1, 3, and 5 forced days.

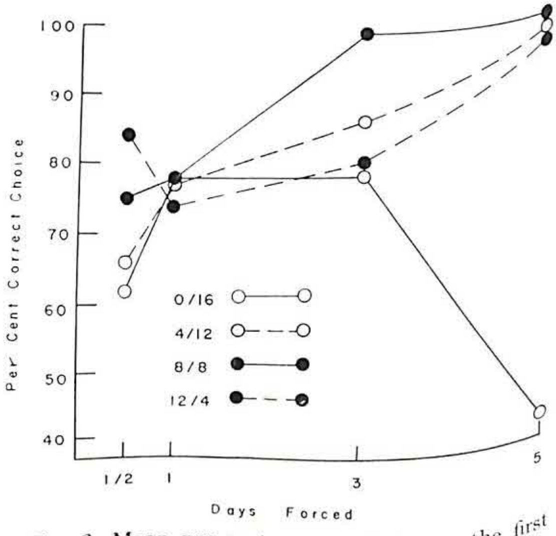

FIG. 2. Mean per cent correct choice on the first free-choice day for the ratio groups 0/16, 4/12, 8/8, and 12/4 over ½, 1, 3, and 5 forced days.

TABLE 2

Analysis of Variance of Transformed Per Cent Correct Scores on the First Free-Choice Day for the Four Ratio Groups Over the Four Forced-Day Levels

Source	*df*	Mean Square	*F*
Days	3	5.9251	11.094
Ratios	3	4.5825	8.580
D × R	9	1.6032	3.002
Within cells	68	0.5341	
Total	83		

TABLE 3

Analysis of Variance of Transformed Per Cent Correct Scores on the First Free-Choice Day for Ratio Groups 4/12, 8/8, and 12/4 on Forced Days 1, 3, and 5

Source	*df*	Mean Square	*F*
Days	2	7.4565	8.996
Ratios	2	2.8266	3.410
D × R	4	0.3358	<1
Within cells	36	0.8836	
Total	44		

the Days Forced × Ratios interaction is approximately 1.

The per cent correct choice for the 16 trials of the first free-choice day for the four ratio groups over the four forced-days levels is shown in Figure 2. The number of animals forming the basis for each point is the same as for the response speed data. A marked tendency for the 0/16 ratio group to diverge more and more from the other ratio groups as forced training progressed may be noted. The poor performance of the 0/16 group after five forced days is due to all three animals.

According to Hull (3), the relationship between the normal deviate corresponding to per cent correct choice and Diff. $_s\bar{E}_R$ is linear. Thus, each animal's per cent correct score was transformed to a normal deviate score and analysis of variance, summarized in Table 2, applied to the transformed scores.

The analysis, including the 0/16 ratio group, shows the main effects for Ratios and Days Forced highly significant ($p < .001$) and the D × R interaction significant beyond the .01 level. In view of the significant interaction it was decided to analyze the 4/12, 8/8, and 12/4 ratio groups both for ½ day forced and for 1, 3, and 5 days forced. The simple Between Groups-Within Groups analysis for ½ day forced indicated that the three ratio groups differ ($F = 6.387$ for 2 and 15 *df*, $p < .01$) on Diff. $_s\bar{E}_R$, with the 12/4 ratio demonstrating the largest difference. The analysis of variance of the factorial design combining the 4/12, 8/8, and 12/4 ratio groups with 1, 3, and 5 forced days is summarized in Table 3. The nonsignificant D × R interaction was pooled with the within-cells to test the main effects. The ratio groups differ ($p < .05$) with the same rank order of size of Diff. $_s\bar{E}_R$ (i.e., 8/8, 4/12, and 12/4) as was found for the response speed data. The main effect for days forced is significant ($p < .001$).

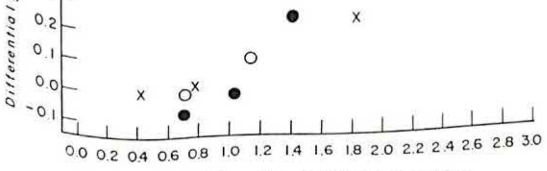

FIG. 3. Mean differential $_s\bar{E}_R$ computed from differences in response speed to the positive and negative cue at the end of forced training plotted against mean differential $_s\bar{E}_R$ computed from per cent correct choice on first free-choice day.

The consistency of the two estimates of Diff. $_s\bar{E}_R$ may be seen in Figure 3, which is a plot of the ordinate values of Figure 1 against the mean of the transformed scores corresponding to the points of Figure 2. The Pearson product-moment correlation between the response speed estimate and the per cent choice estimate, based on the 63 animals in the 4/12, 8/8, and 12/4 groups, is .71. This value may very well be depressed by the ceiling imposed on the estimate of Diff. $_s\bar{E}_R$ by the limitations of the per cent correct choice measure.

DISCUSSION

The hypothesis that differential ratios of forced nonreinforced trials to reinforced trials should result in differential proficiency on a discrimination problem is borne out by both the response speed and per cent correct choice data. Under the conditions of the present study the 8/8 ratio was optimal, but it is to be expected that the optimal ratio is a function of such factors as conditions of reward and nonreward or punishment and procedures and extent of pretraining. For example, the superiority of the 12/4 ratio group on per cent correct choice after ½ day of forced training may indicate that the pretraining developed the strength of the approaching tendencies to the point where, for eight forced trials, a nonreinforced trial to the negative cue led to a greater difference in approaching tendencies to the two cues than did a reinforced trial to the positive cue.

The assumed Hullian relationships between differential response speed and Diff. $_s\bar{E}_R$ and per cent choice and Diff. $_s\bar{E}_R$ gain support in this study from the correlation of .71 found between the two estimates of Diff. $_s\bar{E}_R$. Very similar results have been reported by Logan (5) in the context of a delay of reinforcement study.

SUMMARY

Four ratios of the number of forced nonreinforced trials to the negative cue to the number of forced reinforced trials to the positive cue (0/16, 4/12, 8/8, and 12/4) were combined with four degrees of forced-trial running (½, 1, 3, and 5 days) to test the expectation that different ratios should result in differential magnitudes of approaching tendencies for the two cues on a black-white discrimination problem involving rats. Latency of response to the two cues at the end of forced training and percentage of correct choice on the first free-choice day yielded two experimentally independent measures of Diff. $_s\bar{E}_R$. Significant differences among ratio groups for both measures confirm the hypothesis. The correlation of .71 between the two estimates of Diff. $_s\bar{E}_R$ support the Hullian assumptions relating latency and per cent choice of response to $_s\bar{E}_R$.

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A COMPARISON OF PLACE AND RESPONSE LEARNING IN VERY YOUNG RATS

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Considerable evidence has been accumulated to show that opportunities for visual learning play an important role in the ability of the adult rat to solve complicated spatial orientation problems, such as the Hebb-Williams tests (e.g., 4, 5). The fact that animals which had lived in visually impoverished environments were inferior in such problem-solving to animals raised in more variegated surroundings strongly suggests that visual learning plays an important role in the ability to make use of spatial visual cues. In fact, Forgays and Forgays (4) suggest that such inexperienced rats are less able to use spatial cues. These deprivation studies have pointed to the dependence of *complex* spatial learning upon visual development; they have not investigated the importance of development for *very simple* spatial learning.

Research on simple spatial learning shows that, for adult rats, "place" or "direction" learning is superior to "response" learning when the rats are required to learn a double-T maze situated in a visual environment containing marked extramaze stimuli (1, 6, 7, 8).[1] The first experiment in this area (7) employed a T maze with opposite starting alleys (double T). This technique makes it possible to compare the performance of animals which can learn only by orienting to extramaze cues (place learners) with that of animals which *may* learn either by: (*a*) forming a particular turning response to the choice point, ignoring changes in extramaze cues; or (*b*) learning two different place or direction dispositions (so-called response learners). The present authors interpret the inferiority of response learning to mean either that adult rats find it difficult to ignore shifting extramaze cues, or else that response learning is less efficient than simple place learning. Either interpretation leads to a conclusion that adult rats solve such problems by orienting to general spatial relations rather than by forming absolute stimulus-response connections.

The problem of the present study concerns the ontogeny of such simple place learning. It is possible that rats, as soon as they can see, naturally tend to orient to spatial relations. On the other hand, it is also possible that young rats initially form specific responses to particular environmental stimuli, and that response to spatial relations, even of a simple nature, must await further development. Deese (3, p. 77) suggests that it is ". . . very likely, [that] in early infancy, the rat learns simple stimulus-response units, in the manner suggested by classical conditioning experiments. It is only after a considerable amount of generalization and subsequent discrimination that the rat can free itself from 'pure' stimulus-response learning." Stating the problem more specifically, perhaps response learning is more primitive ontogenetically than is place learning. Very young rats, if they tend to form absolute turning tendencies rather than to orient to spatial relations, ought to learn more efficiently as response than as place learners. It is this hypothesis which the following experiment seeks to test.

METHOD

Apparatus

The experiment was conducted in a room $8\frac{5}{6}$ ft. by 9 ft., containing five stools, two chairs, two windows covered by a black curtain, all opposite the door, a long table placed along the right side of the wall from the door, and a table on which rested an audio-oscillator to the left of the door. The table along the right wall contained miscellaneous apparatus. The room had white tile walls, a gray concrete floor, and an overhead light, situated approximately over the choice point. An elevated wooden double-T maze, painted medium gray and made of boards $2\frac{1}{2}$ in. wide, resting on two stools, stood in the center of the room. The distance from S_1 to S_2 was 2 ft.; the distance between the goal boxes was 4 ft. The goal boxes were enclosed and were 13 in. long, 5 in. wide, and 6 in. deep. Each contained a small glass dish filled with Laboratory Chow in powdered and solid form. A black curtain covered the entrance to each goal box. The rat living cages were kept in a room separate from the one which contained the maze.

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[1] Blodgett, McCutchan, and Mathews (2) distinguish between place and direction dispositions. The present authors regard "direction" disposition as a simpler way of orienting to extra-maze spatial relations.

Subjects

Sixteen albino rats, nine males and seven females, were used. Three females and five males were assigned as place learners. Four females and four males were assigned as response learners.

Procedure

The rats' eyes opened by the eighteenth day after birth. On days 19, 20, and 21, *S*s were handled for half an hour each day in order to tame them.[2] They were weaned into individual wire mesh cages on the twenty-second day. On days 22 and 23, they were placed for 20 min. in each goal box and permitted to eat. A deprivation schedule was begun the evening of the twenty-second day, when all food was removed from their cages, as it was each night during the experiment. The deprivation period was about 10 hr. All animals were 24 days old when the training trials began; six trials a day were given between 8:30 A.M. and 1 P.M. Before each day's series, the maze was rotated 180° to make learning on the basis of intramaze cues impossible. The rats were run in a different order each day.

The goal box to which each place learner was assigned was determined by putting the rat at the choice point. The box toward which it turned was blocked by placing a piece of linoleum behind the curtain, and the opposite goal was designated as correct for that rat. The response learners were arbitrarily assigned the direction in which they were always to turn. A set order of starting positions was assigned to each rat, S122112 or S211221. All trials were conducted using the correction method. The rat was lifted out of its cage and placed at the starting point. After entering the correct goal, it was allowed to remain until it had eaten for 1 min. It was then lifted from the goal gox and replaced in its living cage for about 45 sec. before beginning its next trial. An error was recorded whenever the rat turned a body length in any direction from the choice point other than the correct one. The criterion for learning was ten consecutive errorless trials. No pretraining on a maze runway was given the *S*s, since the intention was to investigate their performance with as little prior spatial learning as possible.

The experiment was conducted in two parts. Nine animals were run in June, 1954, and the remaining seven in July. One animal became ill the first day it was run and had to be replaced.

RESULTS

All eight place learners reached the criterion in 4, 8, 8, 9, 10, 17, 25, and 38 trials, respectively; five of the response learners reached criterion in 7, 10, 15, 32, and 37 trials. (All scores are exclusive of criterion.) Three response learners had not reached criterion when their training was stopped at 72 trials. Of these latter, two rats displayed a strong left-turning tendency, and the third, a tendency to go to Goal 1. Although it had been decided to stop training at 72 trials if learning had not been completed, one rat was run an additional 66 trials (total, 138), just to "see what would happen." It did not reach the criterion, and the only change in its behavior was the substitution of a place bias for its left-turning bias. In the following statistical treatment only the first 72 trials for this animal are included.

The mean number of trials required by the place learners was 14.9; the mean for the response learners was 39.6 trials (the three unsuccessful response learners were assigned a score of 72 trials). The mean difference of 24.7 trials to criterion in favor of the place group yielded a *t* of 2.28, significant beyond the .05 level, for 14 *df*.

The difference in the average scores of the place and response learners in this study, although statistically significant, is smaller than the difference found by Tolman, Ritchie, and Kalish (7). There was no overlap at all between the two groups in their study. Several factors may be responsible for the difference between the two studies: (*a*) there may have been individual differences in learning ability; (*b*) artifacts may have occurred, such as less marked extramaze cues in the present study, a smaller maze, different prehandling; (*c*) young rats may find it somewhat easier to ignore extramaze cues than their elders, although place learning is still easier than response learning under these conditions. There is no basis for deciding which of these factors, if any, accounts for the overlap between our place and response learners.

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[2] Particular effort was made to "gentle" the rats because of the results of a preliminary experiment conducted by the authors with the assistance of Miss Rosalie Barnes, of Vassar College. The preliminary experiment was conducted in the same manner as the experiment reported in the body of the text with the following exceptions: only eight, somewhat older, rats were used as *S*s; the sessions were conducted at night; the rats were not tamed at all prior to learning the maze, but were permitted only to eat for 2 or 3 min. in each goal box. None of the four response learners reached criterion. Although three of the four place learners were eventually successful, they required a large number of trials (the smallest number being 32), and were very erratic in eating. The authors decided that the rats' timidity was probably responsible for their poor performance.

The *t* test applied to the mean difference between time per trial (12.4 sec.) yielded a significant value beyond the .05 level, but in favor of the response group. This difference is probably due to the greater number of trials given the response learners. The error difference is insignificant.

CONCLUSION

Very young place-learning rats are superior to very young response-learning rats in a situation employing the double-T maze presented in an environment containing marked extramaze cues. This conclusion is interpreted to mean that young rats which have had a very limited opportunity for visual development find it more natural to orient to extramaze spatial relations than to develop a turning tendency which would require them to ignore or overcome opposing extramaze spatial cues.

SUMMARY

A study, consisting of a preliminary and a main experiment, was conducted to determine the relative efficiency of place and response learning in very young rats situated in a heterogeneous visual environment. The procedure was based on that of Tolman, Ritchie, and Kalish (7), utilizing a 4-ft. by 2-ft. double-T maze placed in a well-lighted room. Eight place and eight response learners, 24 days old, were given 6 trials a day until each had reached a criterion of 10 correct trials or had been given 72 trials. There were two major findings: (*a*) a significant mean difference of 24.7 trials to criterion in favor of the place group; (*b*) the superiority of place learning was less marked for very young rats than for adults, as seen in a comparison of this study with that of Tolman, Ritchie, and Kalish (7).

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SECONDARY REINFORCEMENT AND MAGNITUDE OF PRIMARY REINFORCEMENT

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Considerable effort has recently been directed toward the investigation of variables which influence the strength of a secondary reinforcer. Concerning the role of the amount of primary reward with which the secondary reinforcer was originally correlated, Lawson (2) has lately reported that within the ranges tested by him, this variable fails to affect the strength of a secondary reinforcer. His procedure involved associating a neutral cue with relatively high reward (HR) in one group of rats and with relatively low reward (LR) in another group. The strength of the secondary reinforcing value of the hitherto neutral stimulus was then determined for both groups. In Experiment I, resistance to extinction furnished the measure of secondary reinforcement, while in Experiment II, involving a U maze, the direction of the subject's (*S*'s) choice was the dependent response. Both experiments failed to yield a significant difference between the performance of the HR and the LR groups.

The present experiment explores the role of the same variable but with the potentially more sensitive procedure of correlating, for each *S*, HR with one cue and LR with a different cue. The *S* is then required to choose between the two stimuli on the assumption that any difference in secondary reinforcing strength between the two cues will manifest itself in the development of a preference on *S*'s part.

METHOD

Subjects. The *S*s were 20 experimentally naive, male albino rats, 60 to 90 days of age at the start of the study.

Apparatus. The apparatus consisted in part of a straight alley 92 cm. long, 10 cm. wide, and 14 cm. high. A small T maze was used for testing: length of stem, 45 cm.; combined length of arms, 70 cm.; width, 10 cm.; and height, 13 cm. Guillotine doors began and terminated the arms. In each arm an 8-cm. movable floor section was located 20 cm. beyond the center of the choice point. A slight depression of this section resulted in the illumination of a 7-w. bulb, defining a "choice" during testing. Two pairs of end boxes, 30 cm. long, 10 cm. wide, and 13 cm. high, were also used. One pair was painted black and vertically striped with five 1 cm. white lines; the other pair was colored white. A black reward cup was used with the black end box, and a white dish, flatter and wider than the black cup, occurred in conjunction with the white end box. The straight alley, the T maze, and the first 8 cm. of the end boxes were painted the same shade of gray.

Pretraining. Ten days prior to the beginning of training *S*s were placed on a 23-hr. food deprivation schedule, Purina chow pellets being available for 1 hr./day.

Training. The 20 *S*s were randomly assigned to four groups of 5 *S*s each. Group B(C) received high reward in the black end box and low reward in the white end box; the same was true for Group B(I). The second letter indicates whether *S*s were to be "correct" (C) on test trial 1 (explained below) or "incorrect" (I). Groups W(C) and W(I) received high reward in the white end box.

Training consisted of 70 trials on the straight alley, 8/day for the first five days and 10/day for three days thereafter. Each day half the trials were to the HR goal box and half were to the LR box, an incompletely random distribution being used. On HR trials *S* found five food pellets, each weighing about 69 mg.; only one pellet was found on LR trials, except the first LR trial, when three pellets were given. In order to obtain some indication as to whether *S*s were discriminating between the different reward value of the two goal boxes, on every trial the starting box matched the goal box, with the difference, of course, that food cup and reward were absent from the former. It was reasoned that *S*s should, after sufficient training, respond to the different starting boxes and run faster on those trials where the starting box corresponded to the HR goal box. With the use of microswitches attached to the doors, the time elapsing from the raising of the starting box door until the lowering of the goal box door was recorded on a timer calibrated in units of 1/100 sec.

On a typical trial, *S* was placed in the starting box, and 10 to 15 sec. later, while *S* was facing in its direction, the guillotine door was raised. The *S* remained in the goal box for 30 sec. or until it grasped the last pellet, which usually occurred within the 30-sec. period; *S* was then returned to the carrying cage. To prevent excessive thirst, water was made available halfway through each day's session. From the second through the seventh training day, the entrance to the goal box was curtained off. Twenty to 40 min. after the last trial of the day, *S*s were given food for a 1-hr. period.

The average duration of food deprivation at the start of a day's trials was 21.5 hr.; range, 21.3 to 25.5 hr. The average intertrial interval on trials 2 to 70 was 11.2 min.; range, 7 to 22 min.

Testing. Testing, which occurred on the day following training day 8, consisted of 15 free choices on the T maze. In order to control for such influences as position preferences and the like, the position of the HR and LR end boxes was assigned as follows. On test trial 1, *S*s of Groups B(C) and W(C) found the HR end box whether they turned right or left; these *S*s, in other words, were forced to be "correct" on the first test trial. The HR box thereafter appeared on the side of their first choice. The reverse was true for the B(I) and W(I) groups; regardless of the direction of their first response, they were "incorrect," i.e., they encountered the LR end box. This procedure forces a 50 per cent level of responding on the initial test trial. A response was defined as an entry into an arm sufficient to activate the light connected to the floor panel. As during most of training, the end boxes were curtained off. The length of time spent in the former goal boxes was reduced to 10 to 15 sec. Finally, although the food cups were present in the end boxes, food reward was absent during testing.

Hunger drive at the start of testing was 21.5 hr. The average intertrial interval was 10.3 min.; range 8 to 16 min.

RESULTS

Training. The median score of each *S* on the HR and on the LR trials was calculated for each of the eight training days. The first row of Table 1 gives a daily tally of the number of *S*s whose median on the HR trials was lower than their median on the LR trials. The second row presents the average difference between the LR and HR medians. These differences are quite small and achieve significance only on the last day of training. Taken together, then, it may be concluded that training was of sufficient duration to produce differential responding on the HR and LR trials.

Testing. Table 2 presents the mean number of responses to the side of the HR end box for the four groups. An analysis of variance yields a significant $F (p < .01)$ only for the C vs. I condition. There is a marked tendency for *S*s encountering the LR box on test trial 1 to make fewer "correct" responses as compared with *S*s "correct" on the initial test trial. Thus, the necessity of adequately controlling for the position variable is again indicated (2).

TABLE 1

Comparison of Response Time on HR and LR Trials

	Training Day							
	1	2	3	4	5	6	7	8
No. *S*s with lower Median on HR trials	10	12	9	11	15*	14	16*	15*
Average LR median – Average HR median (sec.)	1.00	.99	−.60	.00	.34	.07	.09	.37*

* Significantly different from chance at <.05 level.

TABLE 2

Table of Means of the 15 Test Trials

	"Correct"	"Incorrect"	Combined Means
Black	9.60	8.00	8.80
White	9.40	8.20	8.80
Combined Means	9.50	8.10	8.80

Our primary interest, however, lies in determining whether the over-all mean exceeds chance expectation, i.e., whether in general *S*s preferred the side of the T maze which led to the former HR goal box. And indeed they did. When the grand mean, 8.80, is compared with chance expectation, 7.50, a t of 4.859 emerges ($p < .001$).

Another measure, one which leads to the same conclusion, can be obtained by considering the number of *S*s that responded to the HR side of the T maze eight or more times. If chance factors alone were operating during testing, we would expect on the average half the *S*s to produce scores above the value of 7.5. Actually, in the present case, 18 of the 20 *S*s yielded scores of 8 or better. Using the binominal distribution, we find the probability of a difference of this magnitude or greater is less than .0004.

DISCUSSION

The present results offer strong support for the position that, when two cues formerly correlated with primary reward are pitted against each other, the magnitude of the antecedent reward is a variable affecting the relative secondary reinforcing strength of the stimuli. Wolfe (3) obtained similar results with chimpanzees. Lawson's failure to find magnitude of reward to be an effective variable could be taken as indication that in some cases at least behavior fails to obey the simple rules of arithmetic. If it is assumed that his "neutral" (N) end boxes had equal reinforcing strength, Lawson's second experiment may be symbolized as follows: $HR - N = a$, $LR - N = b$; since $a = b$, $HR = LR$. While this conclusion follows as a property of mathematics, it may be that for the behavior under study a corresponding property does not exist. It is conceivable, for example, that the factor of overriding importance in the above situation is the circumstance that both the HR and LR *S*s encountered one end box on the U maze in which they had never been rewarded. In the present experiment the stimuli whose secondary reinforcing strength was to be compared were placed in direct competition, permitting the influence of magnitude of primary reward to operate more directly.

As noted earlier, the time spent in the goal box on HR and on LR trials during training was kept constant at 30 sec. This procedure was employed out of considerations of comparability; Lawson (2) held time in goal box constant at 20 sec. However, the point may be raised that, on the LR trials, after consuming the reward, *S* could have engaged in responses (e.g., "frustration" responses) which tended to reduce the value of the LR goal box as a secondary reinforcer, and that the obtained results are to be ascribed to this factor rather than to magnitude of primary reward per se. While the effect of such a variable, if any, cannot be adjudged from the present data, two points should be mentioned. The first is that many of the *S*s also consistently finished eating the high reward well before the 30-sec. period expired, though naturally not as early as was the case for low reward. And second, although many *S*s did in fact display frustration-like responses on the early LR trials, e.g., searching behavior, upsetting of the reward cup, etc., normally this behavior soon disappeared. Typically, *S* went to the cup, ate the food pellet, and spent the remaining time exploring the goal box. Nevertheless, the role of the length of time spent in the goal box deserves further study.

SUMMARY

Twenty hungry rats were given 70 trials on a straight alley over an eight-day period. Thirty-five trials were rewarded with 5 food pellets (HR) in one goal box, while 35 low-reward trials (one pellet) occurred with a discriminably different goal box. Fifteen nonrewarded test trials were then given on a T maze, the HR end box being on one side of the T and the LR box on the other. The mean number of responses to the HR side exceeded chance expectation at the .001 level; 18 of the 20 *S*s tested had eight or more responses to to the HR side ($p < .0004$). It was concluded that, where one secondary reinforcer is pitted against another, the amount of primary reward with which each derived reinforcer was previously correlated is an important variable determining the relative strength of the secondary reinforcers.

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SECONDARY REINFORCING AND MOTIVATING PROPERTIES OF STIMULI CONTIGUOUS WITH SHOCK ONSET AND TERMINATION[1]

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A number of theorists agree that stimuli contiguous to primary need onset acquire secondary drive properties, and that stimuli contiguous with primary need reduction acquire secondary reward properties (6, 9, 11). There is very little experimental evidence, however, to support such a *general* statement. There are numerous experiments which show that stimuli contiguous with *consummatory*-drive termination become secondary reinforcers (3, 4, 5, 14), and there are also a number which indicate that stimuli contiguous with *pain* (shock) onset become secondary motivators (1, 7, 8, 10). No published experiments were found by the writers, however, which indicate that stimuli contiguous with consummatory drive onset become motivators, or that stimuli contiguous with pain reduction become reinforcers. (Following the final preparation of this paper for publication, an experiment [13] was published which obtained positive results on this problem.)

As Seward (12) has indicated, a critical experiment dealing with the former problem would be difficult to design. The latter problem is more accessible to experimental investigation, and provides the subject matter of this study.

Certain experiments in the area of acquired drives bear a superficial resemblance to the present study. As Brown has pointed out, "there are a number of experiments which demonstrate that the cessation of a fear-arousing stimulus is empirically reinforcing" (2, p. 10). This inference is drawn from the observation that *responses* which are contiguous with the abrupt termination of a fear-arousing stimulus tend to be repeated on later occasions. The present study shifts the emphasis from the responses which are presumably learned due to their drive-termination function, to the behavior-eliciting properties which may accrue to *stimuli* which are present at the time of primary-drive (shock) termination.

An analysis of Miller's (8) classical experiment on acquired drives will illustrate the above distinction. Miller shocked animals in a white compartment and then allowed them to escape into a black compartment. On subsequent test trials he found that the "previously neutral cues of the white box were able to motivate the learning of a new response in the same way as do hunger, thirst, and other drives" (9, p. 437). Miller indicates that this response was learned because it was reinforced as a function of the animals' escaping from the fear-producing stimuli of the white box. In this experiment Miller convincingly demonstrated that the shock (white) compartment had acquired secondary motivating properties. His experiment does not indicate, however, the nature of the behavior-eliciting properties accruing to the escape chamber.

The main purpose of this investigation is to test the hypothesis that stimuli contiguous with pain (shock) termination will acquire secondary-reinforcing properties. A second but less important hypothesis, since it has already been confirmed in other experiments (1, 7, 8, 11), is that stimuli contiguous with shock onset will acquire secondary-motivating properties. The following design not only allows the testing of the above hypotheses, but also provides some data on the relative strength and extinction rates of secondary reinforcing and motivating properties accruing to stimuli in a typical shock-escape situation.

METHOD

Subjects

Fifty-three out of 147 male albino rats from 5 to 6 months old reached the two criteria described below, and the basic data of the experiment comprise their responses. The data for the 94 *Ss* that failed to reach criteria will be included only for comparative purposes.

The *Ss* were taken from the colony maintained by the department of psychology at the University of Missouri. They were maintained on a standard laboratory diet of ground stock feed, with unlimited food and water available at all times.

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[1] This article is a summary of a Ph.D. dissertation prepared by the senior author, under the supervision of Dr. Melvin H. Marx, at the University of Missouri.

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TABLE 1

Description of the Different End Boxes Used in the Preference-Test Units

End Box	Brightness	Shape	Size	Material	Floor Design
1	Striped	Octagon	12″ diam.	Wood	Sand
2	Black	Rectangle	12″ x 10″	Wood	Black wood
3	Black	Rectangle	12″ x 10″	Wood	False grid
4	White	Circle	9″ diam.	Tin	White wood
5	White	Circle	9″ diam.	Tin	False grid

Apparatus

Preference and test trials. The preference-test equipment consisted of four units designed for the four experimental groups. Unit SM:B, for secondary-motivator: black, consisted of a black, false grid-floor end box versus a neutral black and white striped end box. Unit SR:B, for secondary-reinforcer: black was made of a black, smooth-floor end box versus the striped end box. Unit SM:W, for secondary-motivator: white, was made of a white, false grid-floor end box versus the striped end box. Unit SR-W, for secondary-reinforcer: white, consisted of a white, smooth-floor end box versus the striped end box. All end boxes had 6-in. square openings and were 8 in. deep. Shavings were always kept beneath the grids. Table 1 shows the brightness, shape, floor design, size, and construction material of the different end boxes.

Each of the four preference-test units included restraining chambers placed directly between the end boxes. All restraining chambers were 6 in. square and 5 in. deep, and were covered with a wire mesh door. Unpainted guillotine doors at the ends of each restraining chamber were linked together by a pulley system which enabled the experimenter (*E*) to open them simultaneously. Each restraining chamber was divided in the middle, with each half corresponding to the floor design and brightness of the particular end boxes being used. An example of the manner in which the equipment was placed together to form a unit is shown in Figure 1.

Training trials. Three different units comprised the training apparatus: (*a*) a black rectangular shock compartment and a white circular escape compartment with a smooth floor, (*b*) a white circular shock compartment and a black rectangular escape compartment with a smooth floor, and (*c*) a black rectangular shock compartment and an identical escape compartment. The different compartments in the training apparatus were of the same brightness, shape, size, floor design, and construction material as the corresponding end boxes in the preference-test units.

The compartments of a training unit were covered with a transparent plastic door at the top, and were separated by an unpainted, manually operated guillotine door. Each unit was constructed so that the shock and escape compartments could be interchanged.

The room was lighted by a 25 w. light bulb located 4 ft. above the choice point of the particular piece of equipment being used, and a dim desk light in the far corner of the room. During all trials a stop watch was used to measure latencies.

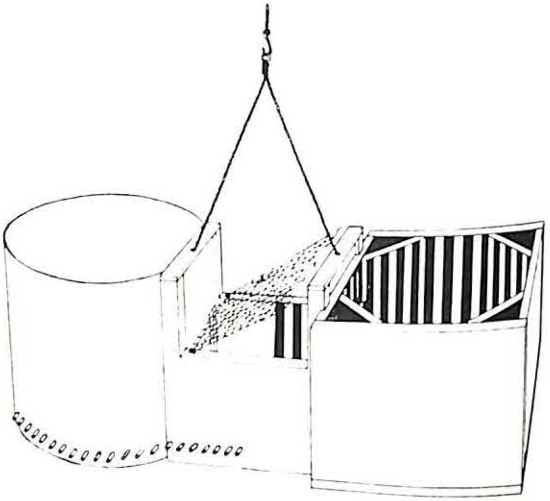

FIG. 1. Unit SM:W of the preference-test equipment.

Experimental Design

Experimental groups. One of the motivation groups—group SM(B), secondary-motivator (black)—was given a series of preference trials in the SM:B preference-test unit, and one of the reinforcement groups—group SR(W), secondary-reinforcer (white)—was given preference trials in the SR:W unit. Both groups were then trained in the black-shock white-escape training unit. They were then tested in the same units in which they had received preference trials.

In order to balance out any preferential factors which might have been present in the preference-test units, two other experimental groups—SM(W), secondary-motivator (white), and SR(B), secondary-reinforcer (black)—were given identical treatment, except that the brightness and other characteristics were opposite to the above during preference, training, and test trials.

It was predicted that the SM groups would tend to avoid the end boxes which were similar to the *shock* chambers, significantly more during test trials than they had avoided the same end boxes during the preference trials. It was also predicted that the SR groups would enter the end boxes similar to the *escape* chambers significantly more during test trials than they had during the preference trials.

Control groups. During the experiment the neutral end box was painted black and white striped rather than gray since gray is theoretically on the black-white generalization dimension. However, since each unit of the preference-test apparatus contained the striped end box, generalization of responses to these black and white stimulus elements became a crucial variable to control in the experiment. Without such a control it would be difficult to say, when testing for reinforcing properties, whether *S* was approaching the end box which was similar to the escape chamber or avoiding the stimulus components of the striped box which were similar to those in the shock chamber. Likewise, when testing for secondary motivation, it would be difficult to say whether *S*s were actually avoiding the presumed

TABLE 2

Treatment, Predictions, and Stimulus Properties Affecting Behavior for All Groups

Group	Pref.	Training From To		Test and Pred.		Properties of Stimuli Affecting Behavior
				Avoid	Approach	
SM(B)	B*–S	B**	W	B*	S	Secondary motivation
SM(W)	W*–S	W**	B	W*	S	
SR(B)	S –B	W**	B	S	B	Secondary reinforcement
SR(W)	S –W	B**	W	S	W	
GC(SR)	B –S	B**	B*	B*	S	Secondary motivation
GC(SM)	W*–S	B**	B*	W vs. S		Neither

* Indicates either a false or inactive grid.

** Indicates an active grid.

B, W, and S refer to black, white, and striped.

motivating stimuli, or approaching the stimulus components of the striped end box which were similar to those in the escape chamber.

Two control groups were used in order to check upon the possible influence of such generalization. Control group GC(SR), generalization control (secondary-reinforcer), was given preference trials in the SM:B unit. Control group, GC(SM), generalization control (secondary-motivator), was given preference trials in the SR:W unit. Both groups were then trained in the black-shock, black-escape unit of the training apparatus. They were then tested in the same units in which they had been given preference trials.

Control group GC(SR) was used to check on the possible generalization of reinforcing properties to the striped box. Since the shock and escape chambers were identical during training, a canceling effect might be expected to take place in relation to the motivating and reinforcing properties accruing to a black grid situation. It was predicted on the basis of data gained from a pilot study, however, that the motivating properties would be more powerful, and that Ss in this group would tend to avoid the black box significantly more during test trials than they had avoided the same box during preference trials. Confirmation of this prediction would indicate that Ss were not responding to reinforcing properties which might have generalized to the striped box, since no white stimulus components were present in the escape compartment during training.

Control group GC(SM) was used to check upon the possibility of generalization of motivating properties to the striped box. With the confirmation of the prediction for control group GC(SR), evidence of generalization should appear in the data of control group GC(SM), if motivating properties were actually generalizing to the striped box. It was predicted that the GC(SM) Ss would tend to approach the white end box no more during the test trials than they had during the preference trials.

Table 2 summarizes the treatment given to all groups, both experimental and control, for all trials, the predictions made for each group, and the stimulus properties which are assumed to affect the behavior of Ss in each group.

Cycles. Since Ss were selected on the basis of criteria, it was decided to run the experiment until at least eight Ss had been obtained for each of the four experimental groups and for each of the two control groups. Six cycles were required before sufficient Ss met both criteria.[3]

Procedure

Preference trials. Five seconds after S was placed in the restraining chamber, both guillotine doors were opened simultaneously. As soon as S's entire body, except tail, was within either end box, the doors were lowered and S was removed from the apparatus.

Each S was given 15 preference trials, 5 trials per day. If S failed to enter one of the end boxes in 5 min. during the first 5 trials, or in 10 min. during the next 5 trials, it was discarded. If S failed to respond in 15 minutes during the last 5 trials, its preference trials were discontinued but it was retained in the experiment. The time criterion was progressively lengthened because it was observed during the pilot study that there was a relatively rapid extinction of the "exploratory drive" in the preference situation.

Between trials Ss were kept in individual isolation cages. Approximately 15 min. elapsed between trials. The positions of the end boxes were alternated according to sequences obtained from a table of random numbers. A record was kept of the choices made by each S following the opening of the guillotine doors. If the choice was in accordance with the hypothesis, it was given a score of 1; if against the hypothesis, it was given a score of zero. On the few occasions when an animal did not make a choice within the time stipulated by the criterion, it was given a score of .5. A record was also kept of the amount of time which each S took in making a choice following the opening of the guillotine doors.

Training trials. Each S was given 25 training trials, 5 trials per day. The S was placed in the shock compartment of the apparatus and the shock (280 w., 500 K. ohm resistor) was turned on immediately. Five seconds later the door separating the shock and the escape compartments was opened. As soon as S made the escape response, the door was lowered. On every trial S was kept in the escape compartment the same length of time that it had remained in the shock compartment.

Between trials Ss were kept in individual isolation cages. Approximately 5 min. elapsed between trials. The positions of the shock and escape compartments were alternated according to a sequence obtained from a table of random numbers. A record was kept of how long each animal remained in the shock compartment on each trial. The response was learned so rapidly that no criterion was needed.

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[3] The data may be found in Table A, which along with Tables B through S, are available from the ADI Auxiliary Publications Project, Photoduplication Service, Library of Congress, Washington 25, D. C. Order Document No. 4643, remitting $2.00 for microfilm or $3.75 for photocopies. Make checks payable to Chief, Photoduplication Service, Library of Congress.

Test trials. The treatment given the *S*s on test trials was the same as that accorded them during preference trials except for the following variations. Each *S* was given 25 trials, 5 trials per day, and an *S* was discarded if it failed to choose one of the end boxes in less than 5 min. twice in succession before it had made at least 20 choices.

RESULTS AND DISCUSSION

Preference and test trials. As indicated in Table 3, the results for the experimental groups were as predicted by the hypotheses. By means of the matched-*t* test, it was found that the shifts between preference and test trials in the choices favoring the predictions were highly significant. When analyzed by comparing preference trials 1 to 15 versus test trials 1 to 15, the difference in the number of choices favoring the predictions for the SR groups yielded a *t* of 3.25, significant beyond the .01 level of confidence. The shift in choices between preference and test trials for the SM groups yielded a *t* of 6.80, significant beyond the .001 level of confidence. Table 3 shows that the shift in choices for particular groups was significant except for the SR(W) group, where a *t* of 2.03 was obtained with 2.36 required at the .05 level of confidence.

Table 3 also shows the above analysis for the control groups. In both cases the results were as predicted; with control groups GC(SR) avoiding the black end box significantly more during test than preference trials, and control group GC(SM) showing no greater tendency to enter the white box during test than had been indicated during preference trials. A *t* of 3.72 was obtained for the GC(SR) group, significant beyond the .01 level of confidence, while the *t* for the GC(SM) group was .24, with 2.31 required at the .05 level of confidence.

TABLE 3

Mean Number of Choices Favoring the Predictions During Preference Trials (1–15) and Test Trials (1–15) for All Groups

Group	Preference		Test		*SE_D*	*t*	*p*
	N	Mean	Mean	Diff.			
SM(B)	8	6.56	12.56	6.00	1.37	4.41	.01
SM(W)	10	7.80	12.05	4.25	.77	5.52	.001
SR(B)	9	6.44	9.89	3.44	1.04	3.31	.02
SR(W)	8	5.62	8.88	3.25	1.60	2.03	—
SM(B)+SM(W)	18	7.25	12.28	5.03	.74	6.80	.001
SR(B)+SR(W)	17	6.06	9.41	3.35	1.03	3.25	.01
GC(SR)	9	7.22	10.14	2.94	.79	3.72	.01
GC(SM)	9	6.11	5.89	−0.22	.90	.24	—

Thus, it is believed that generalization was not an important variable influencing the behavior of the *S*s. The *S*s in the GC(SR) groups could not be said to be responding to the reinforcing properties since there were no white stimulus components present in the training situation. Since the prediction for the GC(SR) group was confirmed, evidence of generalization should have appeared in the data of control group GC(SM), if motivating properties were actually generalizing to the striped box. This was not found to occur.

These findings support the view that stimuli contiguous with pain reduction acquire reinforcing properties and thus provide additional experimental underpinnings for the generalization of the concept "need reduction" in the development of learning theory.

Figure 2 shows the percentage of choices favoring the predictions for all groups during preference and test trials with the data represented in blocks of 5 trials. It will be noted that the curve for the SM groups was consistently higher than the curve for the SR groups on both preference and test trials. However, the shift in the percentage of choices in favor of the predictions was greater for the SM than for the SR groups, after the difference obtained during preference trials was partialed out. A covariance analysis utilized for this purpose yielded an *F* of 7.24, significant at the .02 level of confidence. The variance and regression of these data were homogeneous. It will also be noted from Figure 2 that the rate of extinction

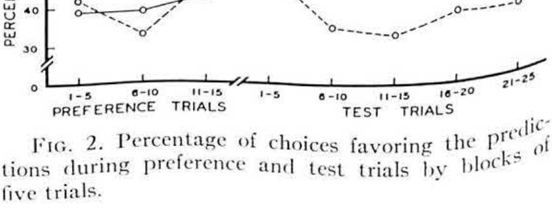

FIG. 2. Percentage of choices favoring the predictions during preference and test trials by blocks of five trials.

was approximately the same for the two groups.

These data suggest that the motivating properties which accrue to stimuli as a function of primary need onset are more powerful in terms of their influence upon behavior than are the reinforcing properties which accrue to stimuli as a function of the termination of the identical primary drive. Although objections may be offered on the basis of presumed inequality of units against making the above comparison, the treatment of the *S*s in the two groups seemed sufficiently similar, not only to allow the comparison, but to justify limited generalization from the results.

During the experiment 44 animals failed to meet the preference-trial criterion, and 50 animals failed to meet the test-trial criterion. Table B (see footnote 3) shows that the choices of the animals that failed the preference criterion corresponded very closely, except where the *N* was extremely small, to the choices made during preference trials by the animals that met the preference criterion. Table C (see footnote 3) indicates that the test trial choices of the animals that failed the test criterion supported the hypotheses in all cases.

These findings are important because they indicate that the *S*s which met the criteria were not in some way selected on the basis of preference factors which might operate to favor the hypotheses.

Tables D and E (see footnote 3) show that few consistent trends were present in the response latency data.

Training trials. All *S*s learned the escape response very rapidly. By trial 15 the average response latency, when analyzed by blocks of 5 trials for each group, both experimental and control, was less than 3 sec. Also, following trial 15, the average response latency of the various groups never differed more than 2 sec. The training data on the animals that failed the test criterion corresponded very closely to those mentioned above. These data are found in Tables F and G (see footnote 3).

Tables H through S (see footnote 3) contain individual data for all animals that met both criteria.

SUMMARY

In order to test the hypothesis that stimuli contiguous with pain (shock) termination will pick up secondary reinforcing properties, *S*s were shocked in a black box and allowed to escape into a white box. It was hypothesized that the shock chamber would pick up motivating properties and the escape chamber reinforcing properties. *S*s were then divided into two groups and tested by placing one group in a discrimination situation where it was simultaneously exposed to a box similar to the escape chamber and a neutral box, and the other group in a like discrimination situation where it was simultaneously exposed to a box similar to the shock chamber and a neutral box. In order to balance out preferential factors, two other groups were given identical treatment except that the brightnesses and other end box characteristics were reversed. The results from two control groups indicated that no generalization occurred.

The results supported the hypothesis that stimuli contiguous with pain reduction acquire secondary reinforcing properties. The shift in the number of choices of the box similar to the escape chamber between a series of preference trials given prior to training and the same box following training was significant at the .01 level of confidence. The shift in choices between preference and test trials was also highly significant for the secondary motivation groups (.001 level of confidence). The data indicated that the curve for the motivation groups was significantly higher (.02 level of confidence) than the curve for the reinforcement groups.

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THE EFFECTS OF INTRAGASTRIC INJECTION OF VARIOUS SUBSTANCES ON SUBSEQUENT BAR-PRESSING

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No generally acceptable theory of the mechanism of food-seeking and food consumption exists today. It seems clear that consummatory behavior itself provides some of the cues for termination of eating, but the cues that initiate food-seeking and eating are still unidentified. A number of possibilities exist, but only two have received much recent experimental support. Mayer (7) has proposed that blood-sugar level provides the cues for both onset and termination of eating. Janowitz and Grossman (5), in summing up many experiments, have proposed a two-factor theory of satiety. Their suggested sources of cues are consummatory behavior and gastric distention, and they conclude that the two sets of cues must act in conjunction.

An experiment by Kohn (6) suggests a technique for obtaining further information on the hunger mechanism. The experiment showed that food injected by fistula directly into the stomach would slow the rate of a subsequent operant response, although the same food ingested by mouth would have more effect on the response. Kohn's "food" was a fortified milk solution, very complex in its physiological action, so that the experiment did not provide much information on the nature of the cues arising from milk in the stomach. It showed clearly, however, that some cue or cues arising after food is introduced into the stomach are important.

The experiments reported here represent an attempt to analyze the phenomenon reported by Kohn. Since we were not concerned with the comparison of oral (taste, swallowing etc.) plus internal factors with internal factors alone, as was Kohn, we did not feel that the fistula was a necessary technique. We used instead a stomach tube, inserted through the esophagus, to introduce substances. Rate of bar-pressing in the Skinner box was our measure of drive. Aperiodic reinforcement with powdered Laboratory Chow provided the incentive.

METHOD

General Procedure

Four experiments using the same procedure are reported here. The *Ss* were male albino rats, Sprague-Dawley strain, three to five months old at the time of testing. The subjects (*Ss*) of the first two experiments were experimentally naive, while those of the second two had been previously used in a T-maze study of secondary reinforcement. The average rate of response under comparable conditions was lower for experiments 3 and 4, so that comparisons between experiments must be made with great caution.

In all experiments the rats were trained, under 22-hr. food deprivation, to press the bar. The usual procedure, after preliminary training, was to give three 46-min. sessions of aperiodic reinforcement on successive training days. Sixteen reinforcements, each approximately $\frac{1}{8}$ gm. powdered Purina Chow, were given during each session. In experiment 3, five days of preliminary APR were given in place of the three of the other experiments, in an attempt to stabilize the rate of responding.

In experiment 1 there were three experimental conditions; in the other experiments, four. The *Ss* served under each condition in every experiment, with one recovery day, spent in the home cages, between experimental sessions. The *Ss* were rotated through the experimental conditions so as to counterbalance any possible sequence effects. A battery of four Skinner boxes was used, and as an additional experimental precaution, each experimental condition was represented in groups run simultaneously. Thus, in experiment 1, *Ss* were run in groups of three, while in the other experiments, there were four to a group. There is no known difference between the boxes, but any possible differences could not influence the means, since each *S* stayed in the same box for all tests, and each condition was therefore represented equally often in each box.

Test substances were introduced through a small rubber catheter, moistened with water and inserted down the esophagus into the stomach. The catheter was attached to a hypodermic syringe, so that pressure could be applied to speed the injection. Handling the group of three or four usually took about 5 min., and the rats were put into the boxes and started 5 min. after the last one was injected. The average time elapsed between injection and the beginning of recording was thus about 7.5 min.

The test consisted of 46 min. of exposure to the bar in a Skinner box. External conditions were exactly the same as in the preliminary training—same aperiodic reinforcement schedule, with the same kind and amount of reinforcement. The experiments thus dealt with the

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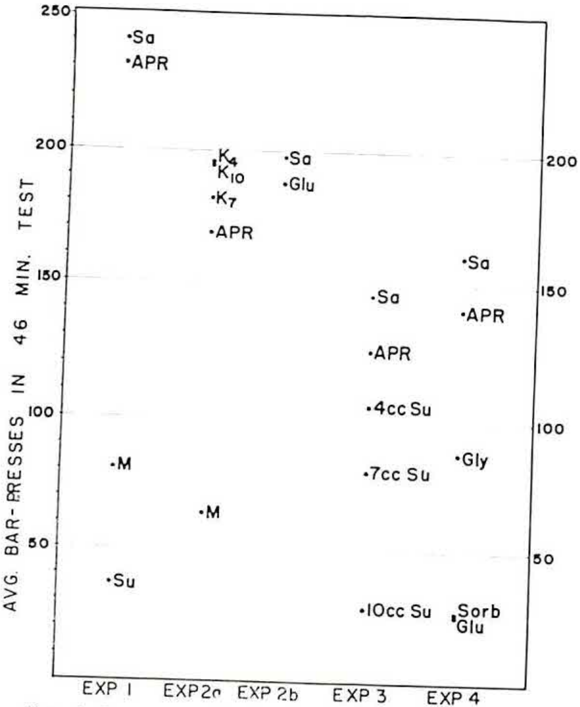

Fig. 1. Summary display of condition means, all experiments. The height of the points above the base line represents the mean number of bar-pressing responses in a Skinner box following intragastric injection as indicated by the label on the point. Responses during test were reinforced aperiodically with powdered chow.

APR—last session of pretest training. Test conditions include: *Sa*—10 cc. normal saline; *M*—10 cc. fortified milk; *Su*—30 per cent sucrose solution; *K*—a suspension of kaolin in water (40 gm. kaolin to 60 cc. water), with the amount of mixture indicated by subscript; *Glu*—glucose (isotonic solution in Exp. 2*a*, molar solution in Exp. 4); *Sorb*—sorbitol, *Gly*—glycerol, each in molar solution, 10 cc.

effects of the intragastric injections on familiar, well-practiced, food-approach behavior.

EXPERIMENT 1

This experiment was designed to check Kohn's results (6), and compare the effects of milk and a simpler nutritive substance, sugar. Twelve male rats were rotated through the experimental conditions. They got 10 cc. of normal saline, 10 cc. of fortified milk (Kohn's formula), or 10 cc. of a 30 per cent (30 gm. sugar to 70 cc. water) sucrose solution.

Results

The injections had a pronounced effect on subsequent rate of bar-pressing. The mean numbers of responses in a 46-min. test period (with variances in parentheses) were: Last day APR, 231.6 (5797); normal saline, 240.8 (7471); sucrose, 37.2 (2562); and milk, 80.8 (11011). The means of this experiment, along with the others, are summarized in Figure 1.

It can be seen from these figures that the injection of saline had little effect on rate. The average number of responses was somewhat higher after saline than on the third pretest day, but this difference is far from significant ($t = .75$). All experiments using saline showed a higher rate following saline than during the pretest period, but this difference probably reflects a trend toward slightly higher rates of response as the experiment progressed, rather than an effect of the saline injection.

Milk and 30 per cent sucrose solution had comparable effects. The rate following milk was somewhat higher than after sucrose, but the evaluation of possible differences between the means is complicated by a significant difference between the variances. Only 7 of the 12 *S*s had higher rates following milk than following sugar, but 3 of the 7 were much higher.

The effects of injection showed up immediately. Average cumulative response curves were almost linear for the whole test period, but the saline curve showed a slight decrease in rate throughout the period, and milk and sugar curves showed a little more. It seems reasonable to say, however, that the effects of injection showed up in the first 2 min. of the test (within 10 min. after injection).

EXPERIMENT 2

Several studies have considered the effect, on subsequent eating, of the direct introduction into the stomach of nutritionally inert bulk. The results are inconclusive, but at least two studies indicate that large quantities of bulk inhibit or reduce food intake (4, 9). It might be added that many patent reducing remedies seem to be based on this theory.

The results of experiment 1 could be interpreted as resulting from bulk in the stomach. Gastric emptying of fluids is controlled in part by the tonicity of the solution. Normal saline, being isotonic, leaves the stomach immediately. The 30 per cent sucrose solution, strongly hypertonic, empties slowly, taking several hours to leave completely. The fortified milk solution is approximately isotonic, but the fats in the milk should slow emptying, as would the other solids.

The purpose of experiment 2, therefore, was to check on the bulk factor. Kaolin, a finely divided clay, was used for bulk. It was suspended in water, 40 gm. kaolin to 60 cc. water, which made a slightly watery paste, just liquid enough to pass through the stomach tube. Several rats were injected with this mixture and then sacrificed and examined. The kaolin began to appear in the duodenum within 10 min., but it emptied slowly, so that more than half of it remained in the stomach for the period of the test. Test conditions consisted of the injection of 10, 7, or 4 cc. of the kaolin mixture, or 10 cc. of fortified milk.

The same 12 rats were used for two additional tests. The first of these was intended to investigate the effect of sugar alone, and used an isotonic solution to avoid stomach distention. Each of the 12 *S*s was used on two days, one with 10 cc. normal saline, the other with 10 cc. of 5 per cent glucose. Order of conditions was counterbalanced.

The second additional test was for duration of the effect. Half the rats were given 10 cc. of 30 per cent sucrose, and the other half 10 cc. of normal saline. They were then put in the boxes for a 4-hr. period. Eight *S*s (4 sugar and 4 saline) were on extinction conditions, and the remaining four on continued APR.

Results

Our choice of milk as a control condition, based on the belief that bulk was a controlling factor, turned out to be most unfortunate. The different amounts of kaolin had no differential effect on response rate, and apparently kaolin itself had none. The means (and variances) were: last day of APR, 168.7 (1248); milk, 64.4 (3456); 10 cc. kaolin, 195.3 (3474); 7 cc. kaolin, 182.6 (6178); and 4 cc. kaolin, 196.7 (7471). On the following test with these same rats, normal saline was used as a control condition, with mean of 198.8 and variance of 5958.

An analysis of variance of the three kaolin conditions showed that the variance associated with condition was less than the rat by condition interaction, indicating no differential effect of kaolin dosage. Comparing the kaolin means with the preceding APR mean and the following normal saline mean (all scores made by the same group of rats), we see no reason to suspect that any kaolin dosage had any effect on response rate. These condition means are summarized in Figure 1.

Milk had about the same effect as it had had in the first experiment. The variance for this experiment was considerably less than in experiment 1 (3456 to 11011), but the difference falls short of the .05 level of significance.

The second test, comparing the effects of isotonic saline and isotonic glucose, showed no differential effect. The mean following saline was 198.8, and following glucose, 187.5. The value of t for correlated scores was 1.10. The slight difference that did exist developed in the last 20 min. of the test.

The last test, dealing with the duration of the effect of 10 cc. of 30 per cent sucrose, showed too much variability to warrant much attention. The data suggest, however, that recovery from the injection begins to take place between 45 and 120 min. after injection.

EXPERIMENT 3

This experiment dealt with the effects of injection of different amounts of the 30 per cent sucrose solution. The *S*s received 10, 7, or 4 cc. of sucrose solution, or 10 cc. of normal saline. Twelve rats were used.

Results

The means (and variances) were: last APR, 125.8 (4058); 10 cc. sugar, 28.8 (1213); 7 cc. sugar, 80.9 (2724); 4 cc. sugar, 105.4 (2385); and 10 cc. normal saline, 146.8 (4632). A plot of these mean response rates against amount of sugar solution (counting the 10 cc. saline as zero sugar) shows the effect to be approximately linear. Cumulative curves showed that the effect was evident in the first 2 min. of the test. The four curves are approximately linear throughout the test period, although the 10-cc. sugar curve does drop off a bit.

EXPERIMENT 4

In this experiment we dealt with the effects of injections of various carbohydrates. The aim was to find a substance that would not enter into metabolism, but would act like glucose in other respects. This aim is not completely attainable, of course, and sorbitol, a sugar alcohol, was chosen. It has the formula $C_6H_{14}O_6 \cdot \frac{1}{2}H_2O$, so that its molecular weight is almost the same as glucose. It has a sweet taste, and has been investigated as a sugar substitute for diabetics. Carr and Krantz, in a summary of the literature (1), conclude that sorbitol is a precursor of liver glycogen, and hence, of blood glucose. Wick and Drury (12) report that sorbitol is not metabolized by the liverless animal. No evidence on rates of absorption or take-up by the liver are available, although Ellis and Krantz (2) report the presence of increased liver glycogen in monkeys 3 hr. after injection of sorbitol by stomach tube. The best guess would seem to be that sorbitol is absorbed more slowly than glucose, but that some was absorbed during the period of the test, and that some was converted to glycogen, and perhaps to glucose.

Glycerol was the second test substance used. It is known to be a precursor of glycogen; in fact, it is converted to glycogen about as rapidly as glucose (8). It counteracts insulin, even if given by stomach tube after the insulin injection, so that its absorption and utilization are probably quite rapid (11).

In an attempt to control gastric emptying time, osmotic pressures of the carbohydrate solutions were equated. The 30 per cent sucrose solution of the earlier experiments was approximately one molar (.988 M), so that 1-M solutions of sorbitol, glycerol, and glucose were used. The *S*s got 10 cc. of one of these, or 10 cc. of normal saline. Sixteen rats were used.

Results

The mean responses per test period (and variances) were: last APR, 140.6 (1575); saline, 160.3 (1833); glycerol, 87.9 (1234); glucose, 25.4 (2319); and sorbitol, 26.7 (1573). See Figure 1 for summary of means. It can be seen that glucose and sorbitol depressed rate of response to an equal extent. Glycerol had a significant depressing effect with respect to saline, but significantly less than glucose or sorbitol.

In an attempt to clarify this difference, we made some crude measurements on rate of gastric emptying for these carbohydrates. Ten cc. of solution was injected by stomach tube. Ten minutes after injection the rat was sacrificed by a sharp blow on the skull, and dissected immediately. The stomach was tied off and removed, and the contents milked into a graduated cylinder. Three rats were used with each solution. The mean contents were: sorbitol, 5.0 cc.; glucose, 5.6 cc.; and glycerol, 3.6 cc. The samples are too small to be taken very seriously, but the results suggest that glycerol empties more rapidly than the other substances.

Cumulative response curves within the hour again were approximately linear, and the differences showed up from the beginning of the test. The glycerol curve showed a slight drop during the 46-min. test period, and the glucose curve rose slightly.

DISCUSSION

The effect of fortified milk on subsequent rate of bar-pressing certainly seems to be a phenomenon subsumable under the normal mechanism of the hunger drive. The milk was a complete diet, and 10 cc. of it gave these rats approximately half their daily caloric requirements. The question might be raised, however, as to whether our investigations of carbohydrate solutions have anything to do with the normal hunger mechanism. The fact that sugar solutions had the same effect on response rate as did milk hardly proves that they did it in the same way.

Since the rat has no regurgitative reflex, direct evidence of nausea cannot be obtained, but a number of considerations lead us to believe it was not present. The linear effect of amount injected, the absence of effect of kaolin, and the different effects of equiosmotic solutions of glycerol and glucose all suggest some other mechanism. So does the fact that hungry rats will readily drink 5 cc. or more of a 30 per cent sucrose solution. We feel, therefore, that we were dealing with the normal hunger-regulation mechanism.

The nature of the mechanism still remains uncertain, however, The experiment with a kaolin preload indicates that bulk alone is not a controlling factor. The absence of an effect following a preload of an isotonic glucose solution suggests that blood glucose alone cannot be the controlling factor. In support of this statement it should be pointed out that there is physiological evidence (10) that absorption of glucose is relatively independent of concentration in the intestine. This statement is a gross oversimplification of a complex problem (3, p. 386), but possible differences in absorption rates from a molar and an isotonic glucose solution could hardly account for the marked difference in their effect on subsequent behavior.

This leaves the possibility of a joint action of two factors—blood glucose and some sort of mechanical distention of the stomach or intestine. The sharp depressant effect of sorbitol casts doubt on this interpretation, since it seems doubtful that much sorbitol was converted to glucose during the period of the test. If our interpretation is correct, it would seem that sorbitol is converted more rapidly than previous evidence indicates. Or, possibly, the sorbitol molecule is sufficiently like glucose to stimulate the cells receptive to glucose.

SUMMARY

Four experiments of the same general plan were reported. All involved measurement of bar-pressing rate in a Skinner box following intragastric injection (by stomach tube) of various substances. The substances were chosen in an attempt to isolate the cue or cues by which the rat is informed that it is hungry.

The results indicated:

1. The introduction of 10 cc. of normal saline by stomach tube has no effect on rate.

2. Ten cc. of a 30 per cent (by weight) sucrose solution had a profound depressive effect on rate—somewhat more than 10 cc. of fortified milk.

3. Ten cc. of a 5 per cent glucose solution (isotonic) had no differential effect from 10 cc. of normal saline.

4. Varying amounts of inert bulk (kaolin) had no differential effect, and no amount seemed to have any effect.

5. The depressive effect on rate is approximately linear with respect to quantity of a 30 per cent sucrose solution.

6. One-molar solutions (equiosmotic) of glucose, glycerol, and sorbitol had different effects. Glucose and sorbitol (a sugar alcohol which is relatively inert metabolically) both had the same depressing effect on rate. Glycerol depressed rate with respect to saline, but not as much as glucose or sorbitol.

As a tentative explanation of these results, it was suggested that two factors, stomach distention and some humoral change, possibly blood sugar, must act in conjunction to reduce drive as measured here. The evidence summarized above was interpreted to mean that neither of these factors could, in isolation, be effective.

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THE MODIFICATION OF SOCIAL DOMINANCE IN A GROUP OF MONKEYS BY INTERANIMAL CONDITIONING[1]

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The conditioned response paradigm has been of some theoretical interest to social psychologists for many years. A number of writers have employed conditioning terminology in speculating upon the development and elaboration of social and emotional responses (7, 10, 11). Others deny the applicability of conditioning principles to social phenomena, at least until sound experimental evidence has been reported (1, 2, 6). The discussions pro and con, about the usefulness of conditioning as a model in this area are somewhat ethereal in that only limited data from experimental social situations are available upon which predictions can be based. Lambert has recently reviewed the theoretical and experimental extensions of S–R theory to social psychology (5).

A previous report (12) described the procedures employed in interanimal avoidance conditioning and provided information concerning the rate of conditioning and extinction. In addition, the amount of generalization of the conditioned avoidance response to monkeys other than the conditioned stimulus was determined as well as the results of the specific discrimination training trials. Briefly, it was found that an avoidance response could readily be established in the monkey using another monkey as the conditioned stimulus; that such an avoidance response did generalize to some extent to other monkeys; and that with specific discrimination training the stimulus animal could be discriminated from other monkeys at a high level.

From the fear-reduction interpretation of avoidance conditioning the conditioned stimulus animal should acquire the property of eliciting fear in the conditioned animal as a result of the repeated association with a noxious stimulus (10). The present experiment was designed to determine whether fear developed by interanimal avoidance conditioning would transfer to another situation and modify the social interactions between the conditioned animal and the stimulus animal.

METHOD

Subjects

A group of eight male and two female adolescent rhesus monkeys were the *S*s in this experiment. The social dominance hierarchy and the nature of social interactions of this group had been studied for a period of approximately 20 months prior to the beginning of this experiment. Previous reports on these animals have detailed the stability of dominance behaviors (8) and the effects of social interactions upon discrimination learning (9).

Apparatus

The apparatus used to establish the avoidance response has been described in detail in a previous report (12). Briefly, it consisted of a large rectangular box divided into two compartments separated by a one-way–vision screen. The floor of each compartment was an electrifiable grid. Electronic control devices enabled *E* to alter the illumination differentials in such a manner as to allow the conditioned *S* to see clearly through the one-way screen into the adjoining compartment where the monkey serving as a conditioned stimulus was present. A delay device presented an electric shock to the conditioning *S* following a 5-sec. exposure of the stimulus animal. The pulling of a bar mounted in the conditioning compartment enabled the animal to escape the shock or to avoid it if the response occurred within the 5-sec. interval. The instrumental response also removed the stimulus monkey from view, i.e., response-terminated stimuli were employed.

Dominance tests were conducted in the Wisconsin General Test Apparatus (WGTA) described by Harlow and Bromer (4).

Procedure

The social dominance hierarchy within the group of ten monkeys had been determined on six separate occasions during the 20 months preceding the present experiment. The dominance relationships had been found to be stable over this period of time (8).

The animal chosen to serve as a conditioned stimulus for pain avoidance for other members of the group was no. 53. His mean dominance rank for the six pretests was eighth in the group (Table 2), and during these same tests he had dominated only one animal (no. 60) consistently and tied with another (no. 59). This monkey was selected because he was low in dominance status, and changes incurred by the independent variable in the direction of an increase in his dominance could, therefore, be of relatively large magnitude. The

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TABLE 1

Animals Conditioned to Avoid the Stimulus Monkey in Successive Conditioning Periods

Conditioning Periods	Animals					
1					57	
2					57	52
3						52
4					57	
5					57	
6	54	55	58	59	60	61
7	54	55	58	59	60	61

relationships within this group have been fully described in the previous report (8).

During conditioning no. 53 was placed in the stimulus compartment of the apparatus. The *S* to be conditioned was placed in the adjoining compartment, which contained the response bar. On a conditioning trial, *E* switched the lighting arrangement so that the stimulus animal was clearly visible from the conditioning compartment. After a 5-sec. exposure of the stimulus animal, a 30-v. electric shock was automatically placed on the grid of the conditioning compartment. The bar-pulling response was facilitated during the initial 30 trials by means of the method of successive approximations (14).

The trials were presented at a rate of 30 trials per day with an average of 60 sec. between trials. To eliminate the possibility that *S* might become conditioned to some cue accompanying the change in lighting arrangement rather than to the stimulus animal, 50 per cent of the trials were control trials. On a control trial the stimulus monkey was removed from the stimulus compartment. The lighting differential was then switched, presenting the conditioning *S* with a view of the empty compartment. This exposure of the empty compartment was terminated by *E* after 5 sec. and, of course, was never accompanied by shock to the conditioning *S*. During the initial five days the control trials were regularly alternated with conditioning trials. Gellermann series were utilized thereafter to intersperse conditioning and control trials (3).

Since it was desired to test the dominance relationships in a systematic fashion throughout the experiment, conditioning trials were arbitrarily run for eight-day periods, then dominance was determined for the entire group of animals on the ensuing five days. This alternating sequence was followed for a period of 14 weeks (seven conditionings and seven dominance tests).

The individual animals which were conditioned to avoid no. 53, and the temporal order of their conditioning is detailed in Table 1.

One additional conditioning was attempted during the experiment. Animals no. 54 and no. 56 had been competitive with each other for second position in the dominance hierarchy for many months. This dominance relationship was known to be flexible and, therefore, would be sensitive to the effect of such an independent variable as interindividual conditioning. As indicated in Table 3, no. 56 had gained ascendancy over no. 54. Consequently, no. 54 was made the stimulus animal for avoidance by no. 56 during conditioning periods 3, 4 and 5 in an attempt to determine whether no. 54 would assume dominance over no. 56 in the social interaction situation.

The specific procedures employed in determining the dominance hierarchy within the group of ten animals was fully described in a previous paper (8). Essentially, each animal was tested for dominance against each other animal in the group in a standardized food-getting situation.

RESULTS

The dominance data for the six tests preceding interanimal conditioning and for the seven tests which occurred between successive conditionings are shown in Table 2. Each entry is the dominance rank achieved by an animal

TABLE 2

The Dominance Ranks of Ten Monkeys on Six Pretests and Seven Tests Taken Following Interindividual Avoidance Conditionings

Animal	Dominance Prior to Conditioning						M	σ	Dominance Tests during Avoidance Conditioning						
	Test								Test						
	1	2	3	4	5	6			1	2	3	4	5	6	7
52	4	4	6	4	5	6	4.83	.92	5	4	6	6	6	5	6
53(CS)	7	9	7	7	8	9	7.83	.92	6	6	4*	4*	3*	3*	4*
54	3	2	2	1	4	3	2.50	.96	3	3	3	3	1	2	2
55	1	1	1	2	2	2	1.5	.50	2	1	1	1	2	6*	1
56	5.5	3	3	3	1	1	2.75	1.52	1	2	2	2	4	1	3
57	2	6	4	5	3	4	4.0	1.30	4	5	5	5	5	4	5
58	9	6	9	6	7	7	7.33	1.29	7	9	10	9	8	9	9
59	8	10	10	9	9	10	9.33	.79	8	7	8	10	9	10	10
60	10	8	8	8	10	8	8.67	.91	10	8	7	7	7	7	7
61	5.5	6	5	10	6	5	6.25	1.73	9	10	9	8	10	8	8

* Rank falls outside fiducial limits of $M \pm 3\sigma$ established from base line of six pretests.

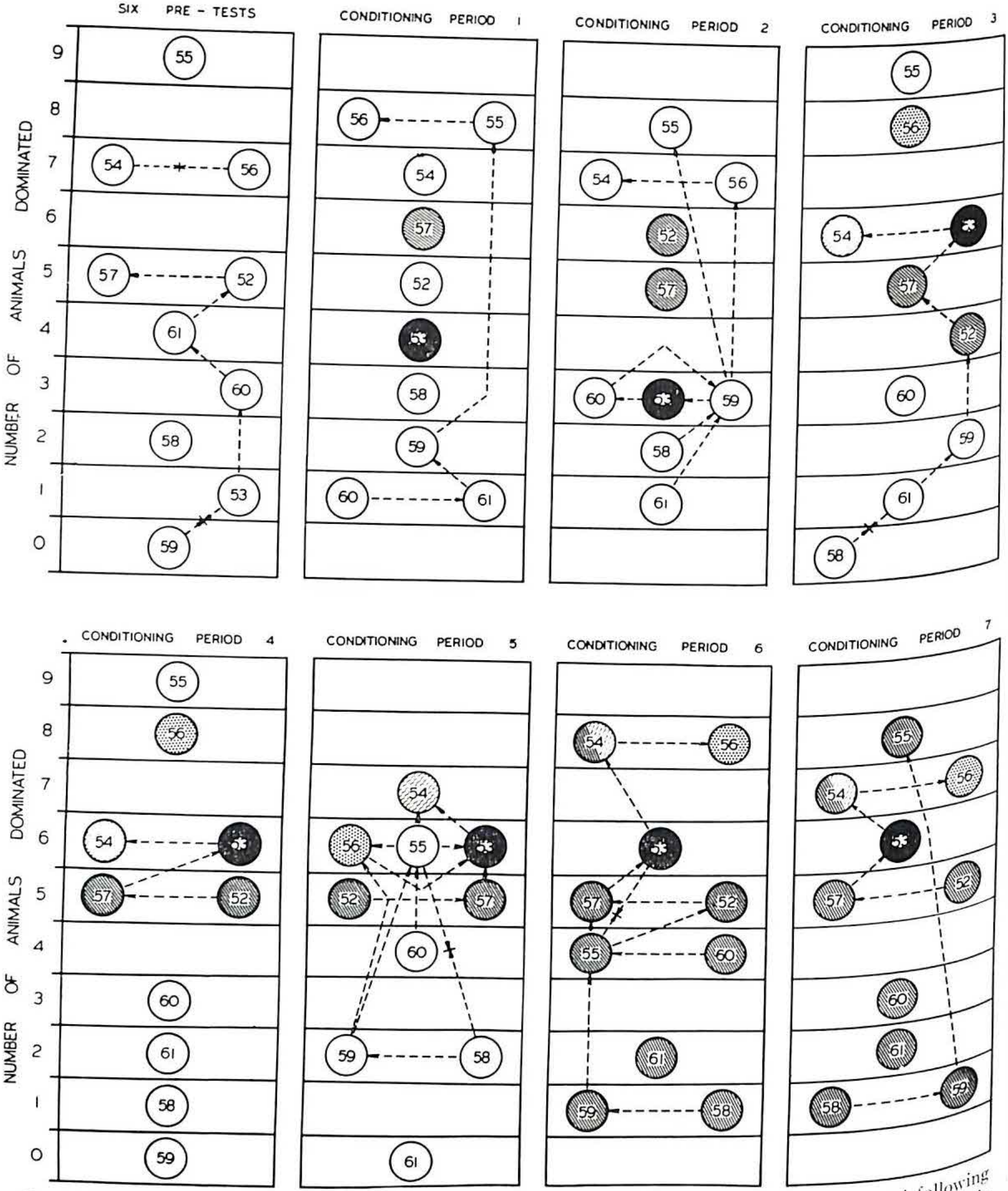

FIG. 1. Sociograms of the dominance relationships within the group of ten monkeys prior to and following successive conditioning periods. Dotted arrows indicate discrepancies in the dominance hierarchy, i.e. animals lower in the hierarchy which dominate animals higher in the group. Ties are shown by joined arrows.

● Number 53, the conditioned stimulus monkey.

▨ Animals conditioned to avoid monkey 53.

░ Number 54, conditioned stimulus for monkey

⠿ Number 56, conditioned to avoid number 54.

TABLE 3

Number of Raisins Obtained by Animals No. 54 and 56 on Successive Dominance Tests

Animal	Pretests						Conditioning Periods							Posttests			
	1	2	B	4	5	6	1	2	3*	4*	5*	6	7	1	2	3	4
54	3	10	7	10	0	0	0	0	2	4	8	8	10	1	0	0	0
56	7	0	3	0	10	10	10	10	8	6	2	2	0	9	10	10	10

* Animal no. 56 conditioned to avoid no. 54 in the preceding eight days.

on a particular dominance test. The most dominant rank was 1, and the most submissive was 10. The animals were ranked on any given test according to the number of competitors dominated on that test. For example, the monkey which secured the majority of pieces of food from the greatest number of other animals in the group was ranked first in dominance. In the event that animals were tied in number of animals dominated during a test, that monkey securing the larger total number of pieces of food was accorded the higher rank.

In order to assess the significance of changes in dominance status subsequent to conditioning, the mean and standard deviation were computed for each individual over the six tests preceding the introduction of conditioning. These data are reported in Table 2. Fiducial limits were obtained by taking $M \pm 3\,\sigma$. The variability of individuals in dominance was found to differ markedly. The ranks achieved on each of the seven dominance determinations during conditioning were evaluated for each individual with the fiducial limits obtained from the premeasures. As indicated in Table 2, the only significant changes in dominance occurred in the increase in status for no. 53 following conditioning periods 3, 4, 5, 6, and 7, and a drop in dominance for no. 55 following period 6.

The detailed dominance relationship following each conditioning period are presented sociometrically in Figure 1. With regard to the results obtained for specific individuals, it was found that the dominance relationships between animals no. 57 and no. 53 were not reversed despite the fact that 57 was given a total of 960 experimental trials (480 conditioning and 480 control). Animal no. 52 became submissive to 53 following the second week of avoidance conditioning trials and remained subordinate to 53 throughout the remainder of the experiment. Following the sixth conditioning period no. 53 was submissive only to no. 57 and no. 56 (an animal never conditioned to avoid no. 53), he tied in amount of food secured with no. 55, and dominated the remaining six animals in the group. Animal no. 55 regained his dominant position over no. 53 on the following test, but all other animals maintained their status with respect to no. 53.

The conditioning of no. 56 to avoid no. 54 resulted in a reversal in dominance relationships following the third week of conditioning trials (conditioning period no. 5). Table 3 includes the results of four additional posttests which occurred during the five months following the last conditioning period. It can be seen that during these posttests no. 56 regained his dominant position with respect to no. 54.

Data concerning the rate at which the avoidance response to another individual is acquired in this apparatus were reported in a previous paper (12). The subjects in the present experiment were not conditioned to a criterion.

DISCUSSION

The effects of interanimal avoidance conditioning were reflected significantly in the dominance behaviors of the animals outside of the conditioning apparatus. The dominance status of the stimulus animal rose significantly from his previous position in the group as other animals were conditioned to avoid him. Moreover, the dominance relationships of another pair of competitive monkeys were found to be altered by the conditioning procedures.

The change in dominance behaviors was not restricted to the specific pair participating in interanimal avoidance but was apparently reflected in the relationship of these animals with other animals in the group. For example, on the dominance test following the third conditioning period, no. 53 was found to have increased in dominance status from his former rank of eighth to a rank of fourth in the group of ten animals (see Table 2 and Figure 1).

Thus, his position had increased four ranks, although only two animals had been conditioned to avoid him. This behavioral change observed in the stimulus animal toward monkeys which had not yet been conditioned to avoid him was striking. The experience of social interaction with animals which had been conditioned to avoid him apparently in some way altered his behavior toward the other subjects. Sears has described interactive changes such as this as attributable to a diadic relationship and stresses their importance in the analysis of social relationships (13).

It was noted in the previous report that monkey no. 59 was considered to be atypical with respect to this dominance test (8). This point can be clarified by reference to Figure 1. This animal consistently obtained a low dominance score in this situation and permitted very submissive animals to take the food. When he did dominate one or more animals, however, they were almost invariably the largest and most dominant members of the group.

SUMMARY

Dominance hierarchy determinations were made on a group of ten rhesus monkeys on six separate occasions. The animal ranking eighth in dominance status in the group was selected to serve as a conditioned stimulus for pain-avoidance by other members of the group. After each conditioning of another animal to avoid the stimulus monkey the dominance hierarchy within the group was retested. It was found that the stimulus monkey increased significantly in dominance status.

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EXPERIENTIAL AND GENETIC FACTORS IN THE ORGANIZATION OF SEXUAL BEHAVIOR IN MALE GUINEA PIGS[1]

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The relative stability of the patterns of sexual behavior displayed by individual male and female mammals has led to speculation and inquiry into the nature of factors that might be responsible for the establishment of such patterns. The possibility that gonadal hormones have an organizing action has long been questioned (1, 2, 4, 15, 19). Genetic factors, on the other hand, may be influential (18). The suggestion has been made also that experiential factors play an important role in primates (5, 9), but in vertebrates below the primates the motor patterns of copulation are said to be innately organized (5, 9, 10, 13, 17). Inasmuch as strains of guinea pigs exist in which the patterns of sexual behavior are relatively homogeneous (18), these strains seemed well suited for a study that would comprehend not only the genetic contribution, but also the possible effect of experience on the development of sexual behavior in a rodent. The investigation was organized as follows: experiment I, in which the role of experience gained during contact with other animals and the influence of the genetic background were studied; experiments II and III, designed for the purpose of obtaining information about the form in which the genetic differences are manifested; experiment IV, in which the effectiveness of male compared with female cage-mates was studied.

EXPERIMENT I

Method

Males of three groups (the isolated males) were placed alone in cages with their mothers from the day of birth until day 25 and isolated thereafter. One group of 17 males was from the inbred Strain 2 (16). Males of this strain are characteristically the smallest animals in the colony, but in their sexual behavior they are moderately vigorous. The second group was composed of 7 males from Strain 13. The males from this inbred strain are large, but generally sluggish behaviorally. The third group consisted of 7 males from a genetically heterogeneous stock. These males are also large, and they are sexually the most vigorous animals in the colony. Control males (the social males) for each of the three groups were raised with their siblings until day 25 when they were weaned. From then until day 73 when they were isolated, they were confined with from 3 to 5 females of the same age.

Beginning on day 77 the sexual performance of the males was determined by seven weekly tests with estrous females of about the same size. The testing procedure and scoring method described by Valenstein, Riss, and Young (18) were used. The number of times a male mounted a female, the number of intromissions and ejaculations, and the amount of the lower measures of sexual behavior (sniffing, nuzzling, and abortive mounts) were recorded. The sexual behavior score takes into account the quantity and maturity of sexual behavior exhibited during a 10-min. test with a female in estrus as well as the length of the interval between the beginning of the test and ejaculation, when ejaculation occurs.

Results

The data obtained from the Strain 2 males (Table 1) reveal a striking difference between the isolated and social males. The difference in average sexual behavior scores is highly significant ($p < .01$). Similarly, the difference in the higher measures of sexual behavior (mounting, intromission, ejaculation) are also significant ($p < .01$) whether the average frequency per animal or the percentage of animals displaying the behavior is considered. Only one isolated Strain 2 male achieved intromission and ejaculation, whereas 16 of 19 social males ejaculated.

When comparing the Strain 2 males with respect to the lower measures of sexual behavior, a different picture is seen. At this level the isolated males surpassed the social males. The former were exceedingly active, displaying a persistent and vigorous interest in the female, but despite this lively interest the isolated males, with one exception, did not mount the females in such a way that intromission and ejaculation could be accomplished.

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TABLE 1

Comparison of Sexual Behavior of Male Guinea Pigs Weaned on Day 25 and Raised in Isolation with that of Males Raised with Females*

Animals		N	Lower Measures		Mountings		Intromissions		Ejaculations		Average Scores
			Average per Animal	Per cent Displaying	Average per Animal	Per cent Displaying	Average per Animal	Per-cent Display ing	Average per Animal	Per cent Displaying	
Strain 2	Isolated	17	149.0	100	1.2	35	0.5	6	0.06	6	3.9
	Social Situation	19	97.3	100	18.0	100	18.0	90	3.7	84	6.8
Strain 13	Isolated	7	129.4	100	2.0	71	0.0	0	0.0	0	3.6
	Social Situation	7	96.4	100	6.4	86	7.6	57	0.6	57	3.0
Genetically Heterogeneous	Isolated	7	70.2	100	17.4	71	12.6	71	4.4	71	7.5
	Social Situation	7	36.4	100	19.6	100	20.6	100	6.7	100	9.9

* Data obtained from 7 tests of each male during isolation, days 77-120.

Differences were seen in the behavior of isolated and social Strain 13 males. To be sure, the average sexual behavior score of the social males was not significantly different from that of the isolated males. On the other hand, an analysis of the individual measures contributing to the sexual behavior score reveals that 57 per cent of the social males had intromissions and ejaculations while none of the isolated males exhibited these higher measures of behavior. The differences analyzed statistically yield a χ^2 of 3.15 (corrected for discontinuity), which lies between the .05 and .10 levels of confidence. However, inasmuch as the difference is in the expected direction, there is justification for using a one-tailed test, which would place the probability below the .05 level. In either case the trend is clear. The lack of a significant difference in average sexual behavior scores is explained by the fact that the socially raised males did not exhibit a sufficiently large number of the higher measures of behavior to counteract the greater activity of the isolated males in the lower measures. It was noted further that the periods of inactivity following intromission were unusually long.

A third result was obtained from the heterogeneous males. The differences in average sexual behavior scores and in the separate measures that contribute to the scores of the isolated and social males are not striking. Again, the differences are in favor of the social males, but they are not significant; they are due to the behavior of two isolated males which did not mount, achieve intromission, or ejaculate. The fact that the weight of these two males was less than average suggested an explanation for their poor performance, which was tested in experiment II.

EXPERIMENT II

The hypothesis was tested that the lack of any striking difference in the performance of the genetically heterogeneous males raised in the two caging situations might be explained by the more rapid growth of these animals. It was considered possible that most of the heterogeneous males had acquired the experience they needed for the organization of the complete pattern of sexual behavior before they were weaned, for males of this stock less than 25 days of age have been observed mounting their mothers.

Method

Ten males were left alone with their mothers until day 10, when they were weaned and isolated. Ten control males were weaned on day 10 but kept with three females of the same age until day 73, when they were isolated. As in experiment I, seven weekly tests were begun on day 77. Weaning at 10 days of age seemed to have no ill effect. They were vigorous, and their weights on day 73 were similar to those of the animals weaned on day 25 (558 and 550 gm., respectively).

Results

The differences between the isolated and social males are clearly apparent (Table 2). The differences in average scores and in the percentage of animals displaying behavior in the higher categories are significant ($p < .01$). Again, the isolated animals exhibited a great

TABLE 2

Comparison of Sexual Behavior of Genetically Heterogeneous Male Guinea Pigs Weaned on Day 10 and Raised in Isolation with that of Males Raised with Females*

	N	Lower Measures		Mountings		Intromissions		Ejaculations		Average Scores
		Average per Animal	Per cent Displaying	Average per Animal	Per cent Displaying	Average per Animal	Per cent Displaying	Average per Animal	Per cent Displaying	
Isolated	10	120.8	100	10.6	30	6.5	30	1.5	30	4.9
Social Situation	10	52.9	100	14.3	100	19.6	100	5.3	100	8.1

* Data obtained from 7 tests of each male during isolation, days 77–120.

TABLE 3

Comparison of Sexual Behavior of Isolated and Socially Raised Castrate Strain 13 Male Guinea Pigs Receiving 500γ of Testosterone Propionate per 100 Grams Body Weight per Day*

	N	Lower Measures		Mountings		Intromissions		Ejaculations		Average Scores
		Average per Animal	Per cent Displaying	Average per Animal	Per cent Displaying	Average per Animal	Per cent Displaying	Average per Animal	Per cent Displaying	
Isolated	6	130.8	100	2.8	67	0.7	33	0	0	3.6
Social Situation	7	105.7	100	16.6	100	11.7	86	0.9	57	4.4

* Data obtained from 7 tests of each male during isolation, days 77–120.

deal of interest in the females which is reflected in the greater amount of lower-measure behavior.

EXPERIMENT III

The sexual performance of the Strain 13 males in experiment I was significantly below that of the Strain 2 and heterogeneous males. Perhaps, therefore, the deficiency of some substance such as androgen accounted for the poor performance of these males even in the social situation. If so, large amounts of an androgen might improve the performance.

Method

Thirteen males were castrated the day of birth and injected daily beginning the following day with 500γ of testosterone propionate[3] per 100 gm. body weight. This amount of testosterone propionate is over 20 times that found to be sufficient to restore the precastrational level of sexual behavior in adult castrates (12). Six of the males were isolated from other siblings the day of birth and weaned on day 12. Seven males were left with their siblings until weaning on day 12; from then until day 73 they were caged with three females of the same age. As before, seven weekly tests were begun on day 77.

Results

The average sexual behavior score of the social males was significantly better ($p < .01$) than that of the isolated males (Table 3). In addition the social males in this experiment performed significantly better ($p < .02$) than the intact social males in experiment I (Table 1). They achieved higher average scores and exhibited more of each measure of behavior. The behavior of the castrated isolated Strain 13 animals (Table 3) was not significantly different from that of the intact isolated males in Experiment I (Table 1). It is to be noted that the performance of the socially reared, injected Strain 13 males was still significantly below that of the untreated, socially reared Strain 2 or heterogeneous males in experiments I and II.

EXPERIMENT IV

The contact with other animals in experiments I, II, and III was with females. This experiment was designed to ascertain the influence of contact with males. The results would reveal whether experience gained during possible copulations had contributed to the differences between the social and isolated males.

Method

Ten heterogeneous and seven Strain 2 males were used. As in experiment II, the heterogeneous males were weaned on day 10. The Strain 2 males were weaned

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[3] Testosterone propionate was supplied by Ciba Pharmaceutical Products, Inc.

TABLE 4

Sexual Behavior of Genetically Heterogeneous and Strain 2 Male Guinea Pigs Raised with Males*

	N	Lower Measures		Mountings		Intromissions		Ejaculations		Average Scores
		Average per Animal	Per cent Displaying	Average per Animal	Per cent Displaying	Average per Animal	Per cent Displaying	Average per Animal	Per cent Displaying	
Strain 2	7	112.7	100	18.0	100	26.6	100	4.6	86	8.2
Genetically Heterogeneous	10	75.6	100	16.9	90	11.9	90	3.9	80	6.7

* Data obtained from 7 tests of each male during isolation, days 77-120.

on day 25. Both groups were confined with two or three males of the same age until day 73. Seven weekly tests were begun on day 77.

Results

For every measure of behavior the performance of the heterogeneous males raised with males (Table 4) was intermediate between that of the social and isolated males of this stock. On the other hand, the performance of the Strain 2 males raised with males (Table 4) surpassed that of the males raised with females (Table 1). The lower measures of behavior and mounting were about the same, but the average number of intromissions and ejaculations and the average sexual behavior score were significantly higher ($p < .01$). In this experiment the sexual behavior score of the Strain 2 males was even higher than that of the heterogeneous males, although the difference was just short of statistical significance ($t = 2.05$).

DISCUSSION

The data show that males which have a minimum of contact with other animals have difficulty in mating. Although each isolated Strain 2 male was given seven tests with estrous females, only 1 of 17 achieved intromission or ejaculation. In contrast 16 of the 19 socially reared males ejaculated, and 17 of 19 had intromissions. Among 7 isolated Strain 13 males, none achieved intromission or ejaculation, whereas 4 of 7 in the social group displayed intromission and ejaculation. A similar difference was seen when the isolated and social Strain 13 males given exogenous androgen were compared. Of the heterogeneous males weaned at 10 days, only 3 of the 10 isolated animals had intromissions or ejaculations, but all the social males displayed the full pattern of sexual behavior. The isolated animals gave evidence of being as much aroused by the presence of the female as were those from the social group, and there was no evidence of any emotional disturbance that could have interfered with their display of sexual behavior. The best explanation of these results appears to be that *the sexual behavior of the isolated animals had not been organized into an effective pattern.*

Not all that is involved in the organization of the pattern is clear, but certain observations are suggestive. The socially raised male orients itself rather specifically to the posterior end of the female. If the posterior end is inaccessible, the male will attempt to force the female into a more favorable position. When mounting the female, the experienced male approaches from the rear, placing his chest over her back while simultaneously clasping her sides with his forepaws. The female is held by this clasping grip of the male, and as his genitalia are brought into contact with the female, pelvic thrusts are made. These thrusts usually result in an intromission and sometimes culminate in an ejaculation.

Isolated male guinea pigs exhibit many of the components of sexual behavior, but they are not organized in such a way that copulation is possible. These males pursue the female, but when overtaking her, they frequently circle around, attempting to mount her head or side. The mounts are attempted by leaning one or both forepaws directly against the back or sides of the female whereupon she generally jumps away. The inability of the inexperienced male to properly mount and clasp the female appears to be his greatest handicap in achieving intromission and ejaculation. Once a male has properly mounted a female, pelvic thrusts (coital reflex) are made, and these generally result in insertion of the penis.

The demonstration that in the guinea pig the organization of sexual behavior into an effective pattern depends on contact with other animals, requires a re-examination of the basis for the opinion (6, 9, 10, 13, 14, 17) that in lower mammals such patterns are innately organized. One possible explanation is that the rat, which is the species that has been studied most commonly, does not require learning in order to exhibit the complete sexual act whereas the guinea pig does. If so, the generalization suggested by the experience with the rat was too broad. A second possible explanation is based on the procedure used in the work on the rat; they were weaned at 21 days of age, and isolation was not begun until this time (6, 17). While in neither case is it stated specifically, the implication is given that the animals remained with their siblings and mother up to weaning. The average litter size of eight or nine would afford considerable opportunity for contact with siblings prior to isolation. That such contact may be important is suggested by the fact that rats, despite their immaturity at birth, have been observed to pursue, mount, and clasp other individuals as early as 21 days after birth (10). Perhaps, therefore, the experimental males should have been isolated, at least from their siblings, at an earlier age.

Each of the three strains of guinea pigs has been seen to present a characteristic picture. The heterogeneous animals possessing large size and vigor are ideally suited for a rapid organization of sexual behavior. The Strain 2 males are also vigorous, but their smaller stature may perhaps handicap them in mounting and clasping the female. The inexperienced Strain 2 males in particular tend to place their forepaws directly on the back of the female rather than around her sides. Stone (17) also suggested that size may be important. The Strain 13 males appear to be still different. It is possible that their sluggishness retards both learning and the display of what was learned, although their large size probably aids them in mounting and clasping the female properly. The latter possibility may be the explanation for the large percentage of these males that exhibited mounting even in the isolated group.

An attempt to improve the performance of the Strain 13 males by administering large quantities of exogenous androgen met with only limited success. The performance of the socially raised castrate males receiving androgen was significantly better than that of the untreated males, but it was still significantly below the level of either the Strain 2 or the heterogeneous males raised under comparable conditions. Recently (16) thyroxin was used in an effort to activate males of this strain. The rate of oxygen consumption was elevated, but sexual behavior was not altered appreciably.

The results from experiment IV in which males of Strain 2 and the heterogeneous stock were provided contact with males present a problem. It will be recalled that while the performance of the Strain 2 males raised with males was significantly elevated above that of those raised with females, the performance of the heterogeneous males raised with males was below that of those raised with females. When both groups are considered together, the results indicate that contact with males generally provides sufficient experience for the organization of sexual behavior into a functional pattern. However, it remains to be explained why the heterogeneous and Strain 2 males should be affected differently. A possible explanation is that the sexual behavior of some of the heterogeneous males was suppressed by the inhibiting action of fighting among these heavier and more aggressive animals. At the same time, the Strain 2 males may have been aroused by the great amount of mounting that takes place among males caged together without suffering from the detrimental effects of fighting.

The performance of the males raised with males brings us to the suggestion developed by Beach (5, 8), that sexual behavior has a duality of components or "functions." One of the components is that of "potency" or the "capacity for sexual performance." It would appear to be associated with organized patterns depending on the activity of centers in the brain stem and spinal cord (5). According to one statement, this function includes "the promptness with which mating is initiated, the frequency of copulation, and the rapidity with which ejaculation occurs" (8, p. 288). The other component is "erotic sensitivity" or the "susceptibility to sexual arousal." It would appear to be mediated by a central excitatory mechanism of the forebrain (5).

Development of the concept appears to have followed observations on the copulatory behavior of partially decorticate rats (3, 7, 10). There was a proportional decrease in the percentage of tests in which copulatory behavior occurred, but the number of copulations during each positive test was not affected, even in the lesion-group in which the percentage of postoperative copulators was lowest. As Beach interpreted the results, there had been a decrease in the ease of arousal to the point of the practical abolition of copulatory behavior, but without an effect on the actual copulatory pattern.

The work with the guinea pig also provides evidence for the existence of dual components of mating behavior, the *organization of the sexual response*, which would correspond roughly to the "capacity for sexual performance" as used by Beach, and *sexual excitability*, which would correspond to "susceptibility to sexual arousal." But as we have thought of "excitability," the promptness with which mating is initiated, the vigor with which the mating is attempted, and the rapidity with which ejaculation occurs are a part of this function rather than of organization. The suggestion originated from the observation that an occasional male will achieve complete copulation in only one or two of ten tests with an estrous female, while giving the appearance of being generally indifferent in the other tests. The organization of the sexual response exists, but the level of excitability is so low that copulation usually does not occur. Strain 13 males fall in this category. On the other hand, most males raised in isolation exhibit excitability, but no organized pattern is present and they do not know how to copulate. While it is convenient to regard sexual behavior as comprising two components, it should be emphasized that they do not function independently. The data suggest that the greater the sexual excitability and vigor, the more rapidly organization of sexual behavior takes place. Also, it has been suggested that the ability or inability to copulate successfully (5, 11), affects the level of excitability.

SUMMARY AND CONCLUSIONS

Four experiments were performed in an effort to determine whether sexual behavior is innately organized in the male guinea pig or whether contact with other animals plays a role in its organization into an effective pattern.

In the first two experiments genetically heterogeneous males and males from the highly inbred Strains 2 and 13 were raised in a social (with females) or in an isolated situation. Significant differences were found between the sexual behavior of social and isolated Strain 2 males. Less marked but nevertheless significant differences were obtained with Strain 13 males. There were no significant differences between the social and isolated heterogeneous animals weaned at 25 days. However, when weaning was done at ten days, significant differences were obtained.

An attempt was made to improve the performance of the behaviorally sluggish Strain 13 males by administering androgen to castrated animals. Their behavior was improved over that of the intact Strain 13 males, but the characteristic differences between this strain and the other two was not overcome.

In the fourth experiment males were raised in a caging situation which afforded them contact only with other males except for the lactating sow. In general, male cage-mates provided sufficient experience for the organization of the sexual behavior pattern, although the picture was complicated somewhat by factors of inhibition and arousal which resulted from the caging of males together.

The main conclusions follow: (*a*) contact with other animals has an organizing action on the development of the copulatory pattern of the male guinea pig; (*b*) the influence of contact may be exerted very early in the life of the animal; (*c*) genetic differences between strains of guinea pigs are responsible for differences in the age at which organization of sexual behavior may take place and for the amount of sexual excitement exhibited during tests; (*d*) genetic differences in level of sexual excitement are not overcome by the administration of large quantities of exogenous androgen; (*e*) contact with males as well as with females generally provides sufficient experience for the organization of the copulatory pattern.

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EFFECTS OF HYPOPHYSECTOMY ON BEHAVIOR IN RATS: II. MAZE AND DISCRIMINATION LEARNING[1]

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In our initial study (9) of rats that were hypophysectomized when 40 days of age, and trained on relatively simple mazes, the learning rate was found to equal or be only slightly inferior to that of like-age controls. We shall re-examine this tentative generalization, in the present study, by use of a complex, 24-unit water maze and a 5-unit visual discrimination apparatus.

METHOD

Animals

Males from the Sprague-Dawley strain comprised the groups. Hypophysectomy[2] was performed at the ages of 15, 30, and 35 days. The 15-day group was permitted to remain with their mothers until about 45 days old. They derived some nutritive benefits from nursing beyond the weaning age and also profited from maternal brooding. One control group was used with the 15- and the 30-day and another with the 35-day hypophysectomites; this provided for similarity of preliminary experience and simultaneity of training of each of the H and C groups.

All rats ate ad libitum from a supply of foodstuffs consisting of the following: ground horse meat, Steenbock mixture (finely ground wheat, oats, and yellow corn; powdered whole milk and casein; $CaCO_3$ and NaCl), Purina Dog Chow, fresh orange, carrot, and lettuce. A cake of Morton's salt hung in the cage. Food was never withheld from any group prior to the time it had finished the allotted trials on the water maze. Thereafter, food was withheld from the 35-day group and their controls for a period of about 12 hr. daily, just prior to their discrimination trials. On the latter problem, food was the principal incentive-reward; on the former, it was escape from water.

A marked degree of retardation in physical development of all hypophysectomites became apparent within a few days after their operations. Figure 1 illustrates the body size and conformation of a normal male and two operates (one from the 30- and one from the 15-day group) when all three were approximately 100 days old. As is apparent, the operates are well proportioned. Table 1 gives the mean body weights of the hypophysectomites and their controls at the time each group started their first trial on the water maze. Although the weights of all young hypophysectomized rats increase slowly for a period of two or three weeks after the operation (7), they then remain relatively constant for periods of time greatly exceeding the total duration of the present study. Coarse guard hairs are conspicuous on the sides and back of normal males at the age of 100 days, but only soft, fine hair similar to that covering a suckling rat of from three to four weeks of age was found on the operates. The genitals of the control had grown to adult-like proportions, while those of the operated animals remained infantile, or regressed toward those of suckling males in the age range of 20 to 25 days (see Fig. 2). Our normal rats at 100 days of age rarely engage in playful wrestling at the morning feeding hour or when the lights are turned on at night; the hypophysectomites, however, jump about and playfully assault each other in the manner so conspicuous in weanlings.

At necropsy the brains of the hypophysectomized animals were so lifted from the base of the skull that the proximal stalk of the infundibulum could be seen, if present, and any remnant of the hypophysis recovered. The scrotum was inspected to determine where the testes usually rested: i.e., in the abdominal cavity, partly descended, or in the distal part of the scrotum. The penis was exposed to estimate the growth of the glans. The abdominal cavity was so opened as to reveal *in situ* the seminal vesicles and coagulatory glands. Samples of the ductus deferens and testis were examined microscopically for spermatozoa. If any of the primary or accessory sexual organs showed evidence of growth, rather than arrest or regression, we assumed that a remnant of the anterior pituitary lobe was functional, even when none was found. Figure 2 contrasts the gonads and accessory organs of a normal control (right) with those of a 15-day, cleanly hypophysectomized male (left) and one from the same group which had a small remnant of the anterior lobe.[3]

Four males suspected of being incompletely hypophysectomized were tested for copulatory activity with small receptive females. The tests were negative, although it is reasonable to assume that, given additional time and tests, some of them might have demonstrated potency later on.

Learning Tasks

A 26-unit swimming maze was used to test the three operated groups and their normal controls; in addition, a 5-unit serial light discrimination problem was provided for the 35-day group and their controls. In Table 1

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[2] Hypophysectomy performed by the Hormone Assay Laboratories, Chicago, Ill.

[3] We are indebted to Dr. Hadley Kirkman, Director of the Anatomy Department, and to his technician Miss Marilyn E. Robbins, for inspecting the heads of the hypophysectomites and sectioning suspicious-looking remnants found at the site of the sella.

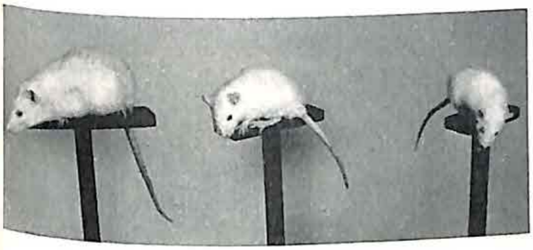

FIG. 1. Normal and hypophysectomized rats, all approximately 100 days old. From left to right the animals are normal, 30-day operate, and 15-day operate.

TABLE 1

Chronological Ages of Groups at Start and Finish of Learning Tasks

Groups	N	Chronological Age			
		Start of Maze	End of Maze	Start of Discrim.	End of Discrim.
15-day hyp.	15	62 (49)*	101		
30-day hyp.	15	53 (85)*	92		
15 & 30 day ctrs.	18	44 (173)*	83		
35-day hyp.	18	66 (88)*	90	100	119
35-day ctrs.	18	66 (223)*	90	100	119

* Mean weight of group (gm.) at start of maze trials.

will be found the chronological ages of each group at the start and finish of the learning tasks. Although there are small age differences between groups, it is presumed that these would not be sufficiently large to influence the performance of normal rats in the age ranges used.

Maze. The floor plan and elevation of the water maze are shown in Figure 3. It is made of galvanized iron and set in a large copper tank. Walls are 15 in. high. To limit, but not entirely prevent retracing, doors may be closed at the four positions indicated by dotted lines crossing the alleys near the numbers 4, 10, 16, and 24. Each door, being hinged at the bottom, can be closed by pulling a string attached at one corner. Pseudodoors, with strings, were placed opposite each working door to similarize the two ends of the alley from a rat's eye point of view. The over-all length of the true path is 20 ft. Water in the tank was maintained at a depth of from 7 to 8 in. and the temperature fluctuated between 66° and 72° F. The *E* recorded two types of errors: (*a*) entries into blind alleys, and (*b*) retracings. The lengths of the latter vary somewhat in different parts of the maze but each is limited by closing the appropriate door when a retracing starts.

For preliminary orientation each rat was given practice swims in a 10-ft. straight alley. These consisted of four swims daily for five days, given in rotation with five or six others. Before the end of this series the rats usually swam directly to the exit, making few if any attempts to scale the walls en route. Upon completion of each swim the rat was put into a warm container to offset chilling from immersion and evaporation of water from the fur.

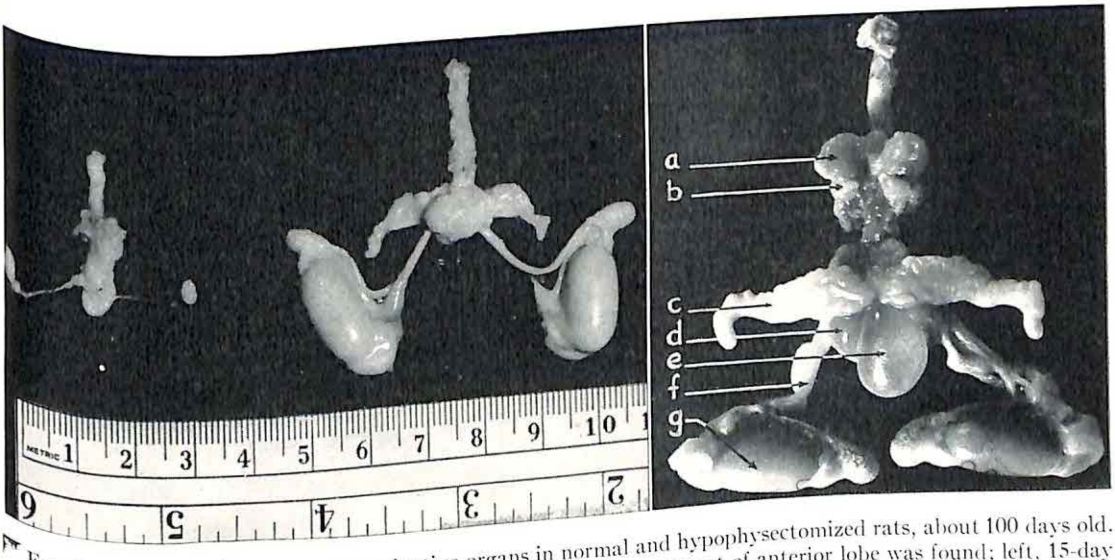

FIG. 2. Primary and accessory reproductive organs in normal and hypophysectomized rats, about 100 days old. At right, normal male; middle, 15-day operate in which a minute remnant of anterior lobe was found; left, 15-day operate in which no evidence of hypophysis remained. Legend: *a*, M. ischio cavernosum penis; *b*, Cowper's gland; *c*, seminal vesicle; *d*, coagulatory gland; *e*, urinary bladder; *f*, ductus deferens; *g*, testis. (Tissues of hypophysectomized animals are soft and pale; hence, clean-cut dissections that preserve all parts of the accessory reproductive tract are difficult to make. From the middle specimen, the M. ischio cavernosum and coagulatory glands were dissected away; in the left specimen, the minute seminal vesicles and coagulatory glands are present but not brought out well by the photograph.)

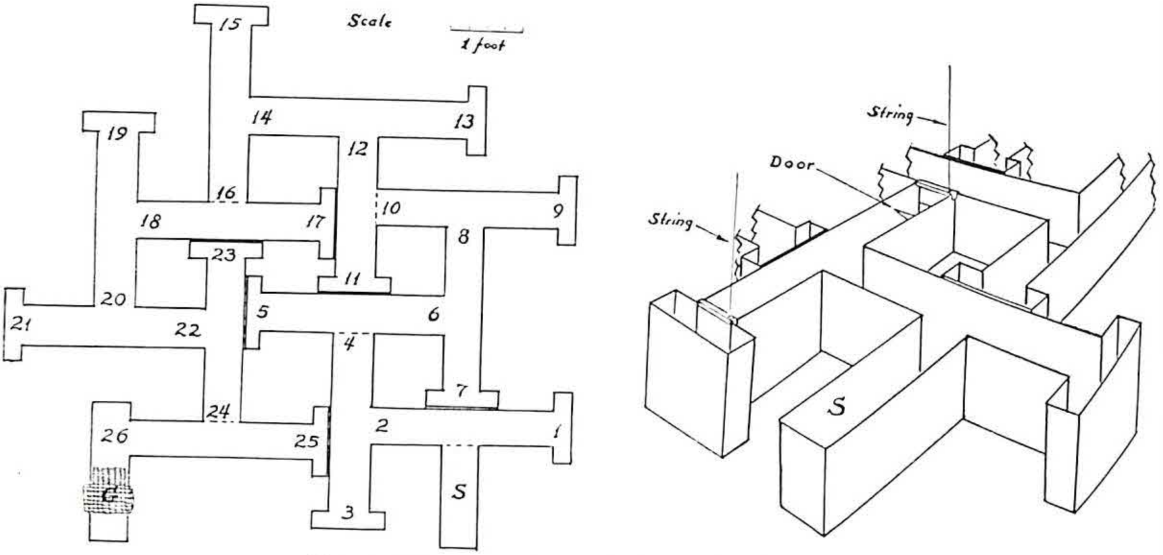

FIG. 3. Thirteen-choice, multiple-T swimming maze.

As said before, no change in food schedule was introduced in connection with the maze trials because escape from water constituted the primary incentive-reward. Probably this was not the only source of motivation, however, because each day, on returning to the home cage, the rat found a supply of fresh food, which had been set into the cage while its group was absent. Most of them began to nibble at the food upon their return to the home cage.

Light discrimination. In this five-unit apparatus (8) the rat had to choose the side of the dark, instead of the illuminated, window. Doors were closed on the side of the bright window to prevent exit from the discrimination chamber and also at the end of each unit to prevent retracings.

As preliminary training the rats were given two trials daily for 5 days in a 10-ft. straight alley, with food in the goal box. Before each day's trial they had been deprived of food for 12 hr. On completion of each run, they were allowed a few nibbles of food. Following the ten preliminary trials, a regular schedule of two daily trials for a total of 20 days was started on the discrimination apparatus. About 10 min. intervened between the two trials, and during this time the rat could eat in a portable goal box. Following the second trial, it received in the home cage the full ration for the succeeding 12 hr.

Two types of errors were recorded: (*a*) attempts to advance on the side of the lighted window, and (*b*) rejection of the dark side after advancing far enough to see that the passageway was open.

RESULTS

Maze

Fifteen- and 30-day operates. One trial daily was given the 15- and 30-day operates and their controls on the maze for 40 consecutive days. The means of forward-going errors are graphically represented in Figure 4. Only those rats that completed the entire 40-trial series are included here. As is evident, there was little difference between the three groups during the first 17 trials, where error elimination was most rapid, although a slight superiority appears to rest with the controls. After trial 17, the graph for the controls clearly separates from the graphs of the operates. As evidence that the early progress of the three groups was very similar, we present in the inset of Figure 4 the cumulative percentages of rats of each group that achieved a criterion of 2 in 3 perfect trials. As is apparent, the three groups hold together very well in respect to this criterion, but what is not apparent is the more rapid improvement by the controls, a fact so clearly evidenced by the latter half of the error curves shown in Figure 4. Noteworthy is the apparent superiority of the 15-day hypophysectomites over the 30-day operates during the latter half of the trial series.

In Tables 2 and 3 will be found the means of forward-going and retracing errors on trials 1 to 20, 21 to 40, and 1 to 40, together with the values of p for differences between the means. No difference between means of forward errors is significant for trials 1 to 20, but on trials 21 to 40 the controls clearly surpass both groups of hypophysectomites. No difference between the operates is significant. In respect

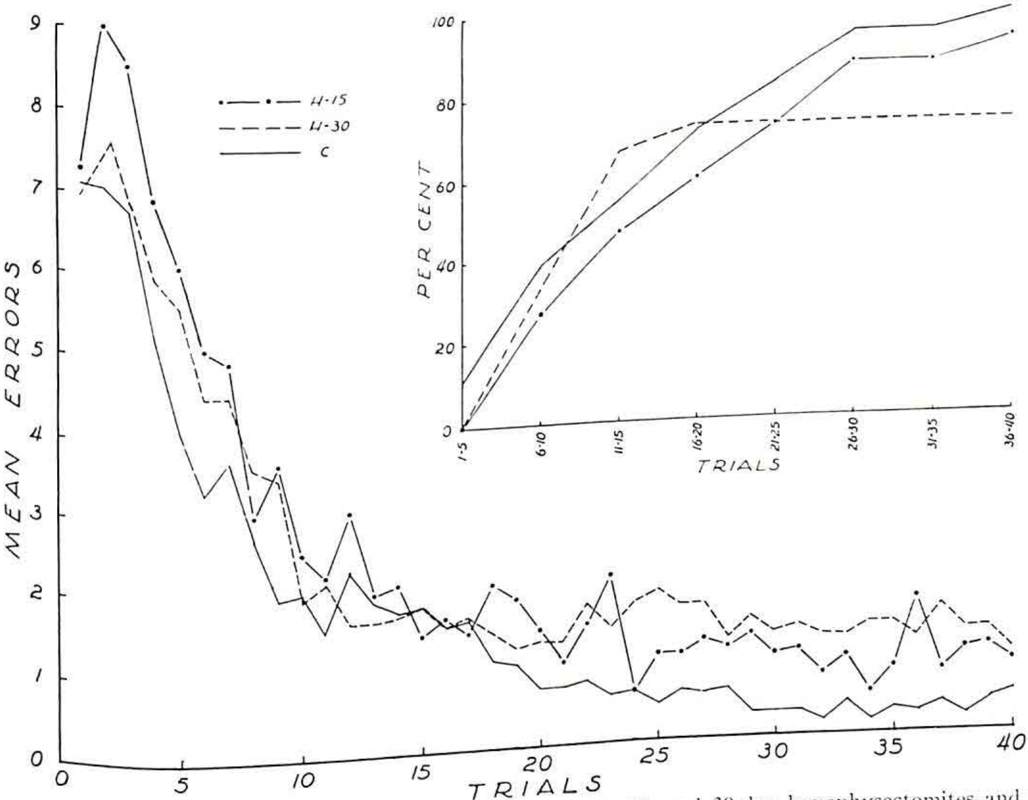

FIG. 4. Graphical representation of forward-going errors from 15- and 30-day hypophysectomites and their controls. Inset at upper right shows cumulative percentages of each group achieving a criterion of two perfect swims in three trials.

TABLE 2

Significance of Differences in Mean Numbers of Forward-Going Errors by the 15- and 30-Day Operates and Their Controls

Groups	Trials 1 to 20			Trials 21 to 40			Trials 1 to 40		
		p			*p*			*p*	
	Mean	15-day	30-day	Mean	15-day	30-day	Mean	15-day	30-day
Controls	59.1	.1	.1	8.1	.01	.001	67.2	.02	.1
15-day	75.9		.1	21.3		.1	97.1		.1
30-day	66.5			27.9			94.4		

TABLE 3

Significance of Differences in Mean Numbers of Retracing Errors by the 15- and 30-Day Operates and Their Controls

Groups	Trials 1 to 20			Trials 21 to 40			Trials 1 to 40		
		p			*p*			*p*	
	Mean	15-day	30-day	Mean	15-day	30-day	Mean	15-day	30-day
Controls	13.3	.01	.1	2.8	.1	.01	16.1	.02	.1
15-day	23.0		.1	5.1		.1	28.1		.1
30-day	14.9			8.6			23.5		

to retracings, less consistency in trends was obtained; the difference between controls and 15-day operates is significant for trials 1 to 20, but not for trials 21 to 40; contrariwise, the difference for the 30-day group is significant for trials 21 to 40, but not for 1 to 20. Again, the differences between the 15- and 30-day groups are not significant.

A study of the raw data throws some light on what was happening in terms of performance by the H animals beyond trial 17. Some operates, after coming close to mastery of the maze, began again to retrace or to enter blind alleys, and continued to do so thereafter; also, some resumed an early tendency to retrace after making a forward-going error rather than to continue in the goalward direction. With each retracing there was an opportunity to make additional forward-going errors. Since evidence of deterioration of performance in normal rats when nearing mastery of a maze usually results from a change in motivation, we may rightfully question whether that factor, instead of genuine inferior ability, caused the relatively poorer progress of the hypophysectomized rats beyond trial 17.

Thirty-five-day operates. Preliminary training of the 35-day operates and their controls was similar to that of the preceding groups. On the maze, however, they were given 2 trials daily for the first 22 trials and 1 trial daily thereafter for 14 additional trials. During the 2-trial period, they had between 8 and 12 min. to rest between trials. An inspection of the performance of the H group up to trial 22 led us to shift from 2 to 1 trial per day for the purpose of determining whether a less fatiguing daily schedule would accelerate improvement in the operates.

Figure 5 presents the learning curves for forward-going errors. It is apparent that the 35-day group, under the conditions of their trial series, was inferior to the 15- and 30-day operates (see Fig. 4). Their plateau-like effect occurred somewhat earlier than was the case with the 15- and 30-day groups. Moreover, the cumulative percentages of 35-day hypophysectomites achieving a criterion of 2 in 3 perfect runs was much poorer than those of the 15- and 30-day operates, as well as poorer than their normal controls.

In Table 4 will be found the means of forward-going and retracing errors together with the values of p for differences between the operates and their controls. Significant differences in forward-going errors for the two- and the one-trial periods are present. For retracings the difference is clearly significant for only the one-trial period (23 to 36). Although additional trials might have brought about some improvement in the operated rats, because most of

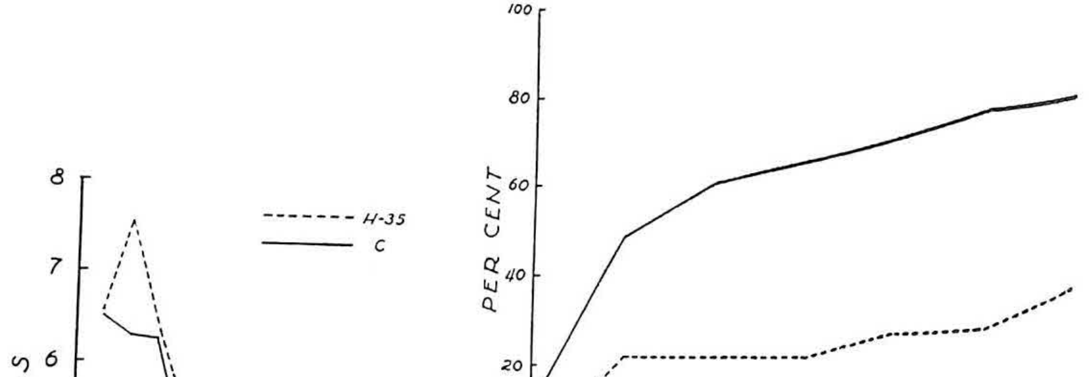

FIG. 5. Graphical representation of forward-going errors from 35-day operates and their controls. Inset gives cumulative percentages of rats achieving two perfect swims in any group of three trials.

TABLE 4

Significance of Differences in Means of Errors for the 35-Day Operates and Their Controls

Errors	Trials	Means		p
		C	H	
Forward	1–22	55.2	83.3	.001
	23–36	10.4	40.4	.001
	1–36	65.6	123.7	.001
Retracing	1–22	15.8	18.9	.1
	23–36	3.6	12.3	.001
	1–36	19.4	31.1	.01

TABLE 5

Comparison of 35-Day Operates and Their Controls on Light Discrimination Habit

Errors	Mean Errors		p
	Controls	Experimentals	
Type *a*	52.9	48.4	$>.1$
Type *b*	13.3	10.8	$>.1$

them had several types of errors to correct, their relative inferiority to the control group would certainly have persisted during many additional trials.

Inspection of individual records suggests that although a considerable amount of stereotypy of errors appeared in records of the controls and operates, nevertheless the patterns of errors were highly individualized. This probably indicates that the difference in performance is not ascribable to any objective feature of the maze per se. If there were a common factor (other than intelligence) affecting the operated rats, e.g., fatigue or discomfort from sustained effort, it would seem that their reactions to this factor ultimately led to the "fixation" of individualized response tendencies which perpetuated rather than eliminated error scores.

Light Discrimination Learning

To shed light on the generality of the inferiority shown by the 35-day operates, they were put into competition with their normal controls in learning a five-unit, serial light discrimination task (8). Their training began within a few days after the last trial on the maze. To orient them to a linear type of run, instead of the circuitous route required by the maze, preliminary training on a 10-ft. straightaway was given. Each animal, in rotation with five or six others, had two trials daily for 5 days. Before each day's trials they had been deprived of food for about 12 hr. and on completion of each run, were allowed a few nibbles of the regular diet. Two trials daily were given on the discrimination problem, with an interval of approximately 10 min. between trials. During that interval the rat was allowed to eat from a dish containing the regular diet. After the second trial it was allowed to eat again for a period of about 10 min. before being returned to the home cage where it could continue to eat ad libitum during the next 11 to 12 hr.

Table 5 gives the means for the *a* and *b* types of errors. The small differences favoring the controls are not significant. Thus the clear-cut inferiority shown by the 35-day operates on the 24-unit maze was not generalized to the discrimination task. Noteworthy is the similarity of this finding and that reported by Stone and King (9) for the elevated maze, where vision plays a large role in performance. Operates that had been somewhat inferior on the swimming maze were not inferior to the controls on the elevated maze.

DISCUSSION

The present study supports our previous report (9) in demonstrating some inferiority in maze performance of hypophysectomized rats on the water maze. To what should this be ascribed?

Probably the small size of the operates has no bearing on the inferiority of their maze performance. Unpublished records on young males 30 to 40 days of age and of approximately the same size as the operates of this study show that they can master the 26-unit maze as rapidly as the older, larger controls of the present study. Also, the revolving-wheel type of inactivity of hypophysectomites (5, 6) appears to have no explanatory value here, for our operates are not less active than the controls in their home cages, on table tops, or on elevated runways when given complete freedom for general activity and exploration. In this respect they appear to confirm the observations of Applezweig and Moeller (1). Likewise, impairment of certain endocrines (gonads, thyroid, and adrenals) which immediately follows hypophysectomy has no certain value for explaining the divergencies obtained. Ablation of gonads, thyroid, or suprarenal cortex has not heretofore adversely affected maze learning ability of rats (1, 4).

The similarity of performance of the 35-day operates and their controls on the five-unit light discrimination test cannot be regarded as certain evidence that differences on the mazes were not caused by impaired learning ability for mazes. In normal rats no correlation between learning scores on these two types of problems has yet been reported. Nevertheless, the similarity of operated and control groups in cue learning is of interest because it is in accord with our previously reported results for the elevated maze where vision unquestionably plays a greater role in choice of pathway than is the case with the high-walled, swimming mazes.

By manipulation of specific experimental variables, either mild or severe deterioration in learning scores of rats may be caused at any stage of the trial series. As a rule these changes can be understood if one assumes that the changes imposed alter the rat's main objectives and, consequently, its direction of effort: changes that lead to the renewal or stereotypy of errors, as defined by *E*. In this study no alteration of procedure was introduced for the 15- and 30-day operates and only a shift from two to one trial per day for the 35-day group was made. The latter should have effected a slight improvement in performance, since one trial daily is usually more efficient than two or more trials. For these groups the change was introduced at trial 22, which is well beyond the time a divergence between the hypophysectomites and controls first appeared. Hence, if a change in motivation did occur in the operated animals, and if it is responsible for a level of performance that falls short of their true learning ability, it must be ascribable to some still undetected factor. Fatigue or discomfort have been mentioned earlier, but it must be admitted that no evidence was obtained to prove that they had a differential effect on performance between groups; and especially difficult would be their use as explanatory concepts unless one could show why they became effective just when they did, especially in the two younger groups of operates when they were near mastery of the maze (trial 17), i.e., at a time when effort should have been decreasing because of progressive shortening of the pathway.

There may be a general impairment of learning ability, as such. If so, this would be in accord with the finding of a slightly lower mean level of "test intelligence" in children and adolescents known to have hypophyseal insufficiency (2, 3). However, the good performance of our 15- and 30-day operates for the first 17 trials, when most of them were near mastery of the maze, raises some doubt as to whether their failure to keep pace with the controls thereafter indicates that they were near the ceiling of their true learning ability, rather than that some self-instigated change in objectives led to new patterns of errors and stereotypy of unfruitful choices. The fact that the best performers of the 15- and 35-day operates and their control groups are very similar justifies further study of the "change in motivation hypothesis" for explaining the obtained differences.

Hypophysectomy of suckling rats (15 days), when cells of the cortex are still undergoing division, did not cause a significant difference from hypophysectomy of 30-day animals in which cell division of the cerebral cortex has already ceased. Whether one can assume that mitosis of cerebral cells proceeds independently of anterior lobe hormone is a relevant question, but it cannot be answered without further investigations that will entail still earlier operations than those herein used. Also, it is pertinent to inquire whether maturation and maintenance of cerebral cells are independent of anterior lobe hormone. It seems obvious from this and our earlier study that retardation and degeneration of the cerebral cortex must be infinitesimal in amount, if any, as compared with that which occurs in the reproductive system and in other endocrine glands under trophic influence of the anterior lobe of the hypophysis.

CONCLUSIONS

1. The learning records of male rats, hypophysectomized at the ages of 15, 30, and 35 days, were significantly inferior to corresponding records of like-age controls during the

latter half or two-thirds of their trial series on a 13-choice swimming maze.

2. No clear-cut difference obtained between those hypophysectomized at 15 days of age, when cortical cells are still dividing, and the 30-day group which was operated after mitosis in the cerebral cortex had ceased.

3. No significant difference was found between the 35-day hypophysectomites and their controls in learning a five-unit light discrimination problem.

4. The principal unresolved question is whether hypophysectomy causes a real deficit in *ability* or merely impairs maze performance through some as yet undiscovered kind of motivational disturbance. Probably the deficit is not caused by the size differential, by difference in exploratory activity, or indirectly by impairment of other endocrine glands over which the hypophysis exercises trophic influence.

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SUBCORTICAL MECHANISMS IN EMOTIONAL BEHAVIOR: THE DURATION OF AFFECTIVE CHANGES FOLLOWING SEPTAL AND HABENULAR LESIONS IN THE ALBINO RAT

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An earlier report (1) presented evidence to indicate that, in rats, surgical lesions of the septal forebrain region can have the immediate effect of increasing emotional reactivity and startle response magnitude while diminishing the strength of a previously conditioned emotional response (CER) of the "fear" or "anxiety" type. In this earlier investigation, all postoperative tests for retention of the CER and magnitude of the startle response were conducted within a few days after surgery, and only the ratings for emotional reactivity were continued for any appreciable period after placement of the lesions. The gradual diminution in emotional reactivity throughout the 12-day postoperative rating period in these earlier experiments suggests that the behavioral changes following such lesions may be of limited duration. Whether time alone, the daily handling for rating purposes, or some combination of the two, was the critical limiting factor, could not be determined from this initial experiment.

The present study was designed to investigate further the specific character of such affective changes following septal ablation and the critical factors limiting their duration. In addition, an attempt was made to explore further the role of other subcortical structures in the elaboration of emotional behavior by preparing and studying the effects of lesions of the habenular complex of the thalamus. Recent anatomical evidence (7) has clearly shown that the habenular nucleus figures prominently among the diencephalic structures which receive direct projections from the septal region and suggests the importance of exploring possible affective behavioral changes following lesions of this nuclear complex.

METHOD

General Procedure

Twenty-six male albino rats, approximately 100 days of age at the start of the experiments, served as *Ss* and were divided into four groups. In Group I (12 animals), lesions were produced in the septal forebrain area *following* acquisition of the CER. In Group II (6 animals), lesions were produced in the habenular complex of the thalamus *prior* to acquisition of the CER. In Group III (4 animals) habenular lesions were produced *following* acquisition of the CER. Group IV acquired the CER and served as unoperated controls. In addition, ratings of emotional reactivity and measurements of startle response magnitude were made for all animals on several occasions before surgery and at varying intervals up to 60 days postoperatively. Tests for retention and experimental extinction of the CER were also conducted at the same postoperative intervals. Upon completion of the experiments, the animals were sacrificed, their brains fixed, sectioned, and stained in order to verify histologically the location and extent of the lesions.

Emotional Conditioning

The conditioned emotional response (CER), as described in the previous report (1), may be characterized as expressing the animal's learned anticipation of a painful event—a mildly painful electric shock. In the present experiment, however, this response was superimposed upon a stable lever-pressing habit according to a procedure previously described by Hunt and Brady (4). In brief, thirsty animals were first trained in lever-pressing for an aperiodic water reward. Then, all animals received a total of eight emotional conditioning trials, each consisting of a 3-min. presentation of a clicking noise (as the CS) terminated contiguously with a momentary electric shock to the feet (approximately 1.5 ma.) as the unconditioned stimulus, delivered through the grill floor of the apparatus. Most of the conditioning trials were spaced several days apart; only one conditioning trial was given on any one day. On intervening days, the animals received normal runs in the lever-pressing boxes with neither clicker nor shock in order to adapt out generalized fear reactions to the apparatus and permit the CER to appear more clearly as a plateau in the cumulative response curve. The reduction or cessation in lever-pressing during presentation of the CS, accompanied by defecation and immobility, constitutes the CER.

The animals received 9-min. recorded runs in the lever-pressing apparatus throughout the course of the experiment. A record was kept of the total number of lever responses made by the end of the third, sixth, and ninth minutes of each run by each animal. On conditioning days, the CS was introduced at the beginning of the fourth minute and terminated contiguously with the UCS at the end of the sixth. Presentation of the CS alone during the second 3-min. segment of a run tested for retention of the CER postoperatively and also pro-

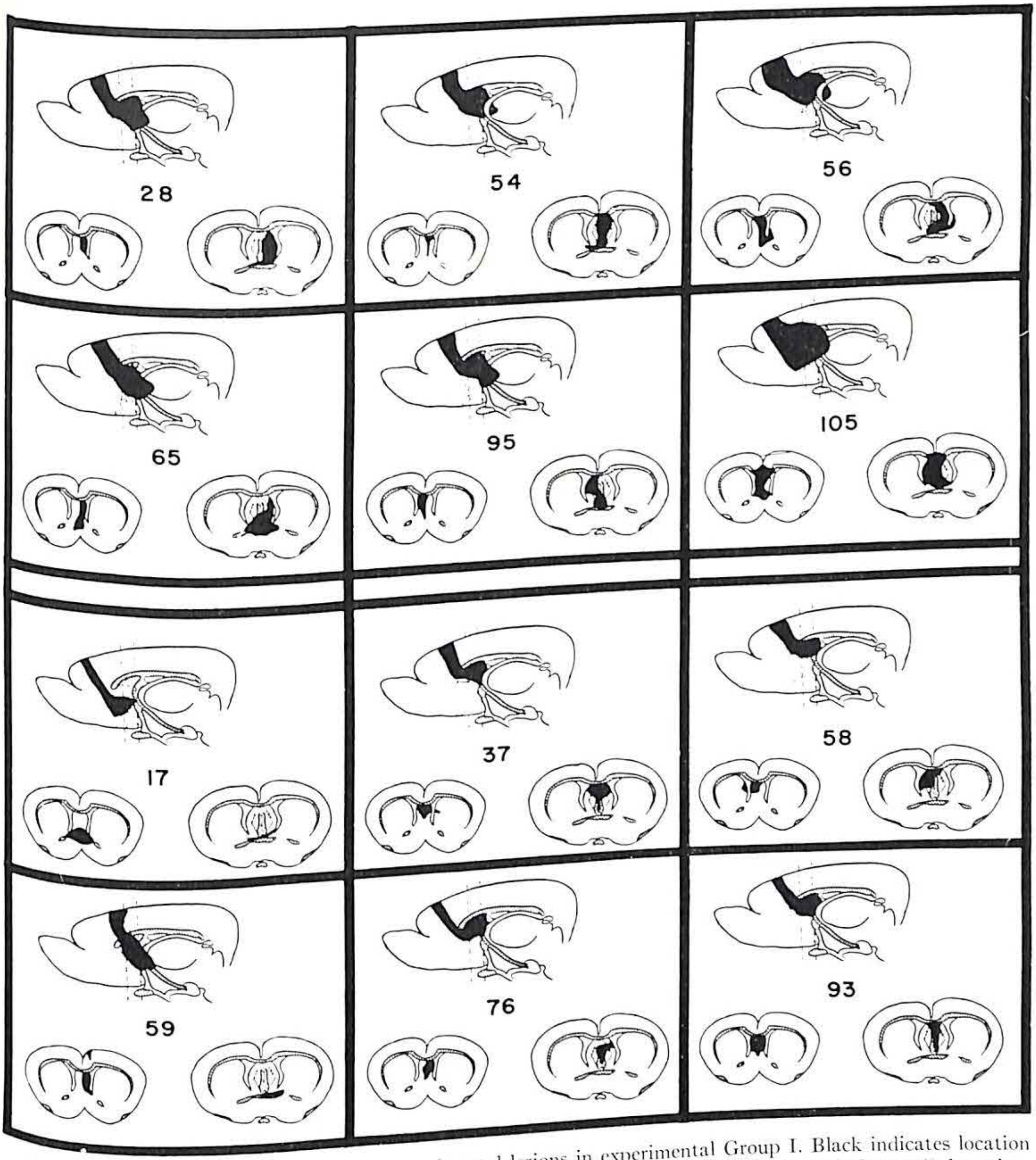

FIG. 1. Medial and frontal reconstructions of septal lesions in experimental Group I. Black indicates location and extent of the lesions in the reconstructions. See Figure 1 in previous paper by Brady and Nauta (1) for orientation.

vided for experimental extinction of the response by a series of such unreinforced trials.

Following acquisition of the lever-pressing response but before conditioning of the CER, habenular lesions were produced in the six animals of Group II. Three days after surgery in Group II, CER training was begun in all animals of all groups.

On the day following the eighth conditioning trial, septal lesions were produced in the 12 animals of Group I, habenular lesions in the 4 animals of Group III, and the remaining 4 animals of Group IV served as non-operated controls. Histological reconstruction of the lesions is shown in Figures 1 and 2. Three days after operation, tests for retention of the conditioned emotional response were conducted with all animals by a 3-min. presentation of the clicker alone.

Emotional Reactivity Rating and Startle Response Measurement

Both the emotional reactivity rating scale procedure and startle response measurement technique were identical to those used in the previous experiment (1). Ratings were made of all animals on seven different

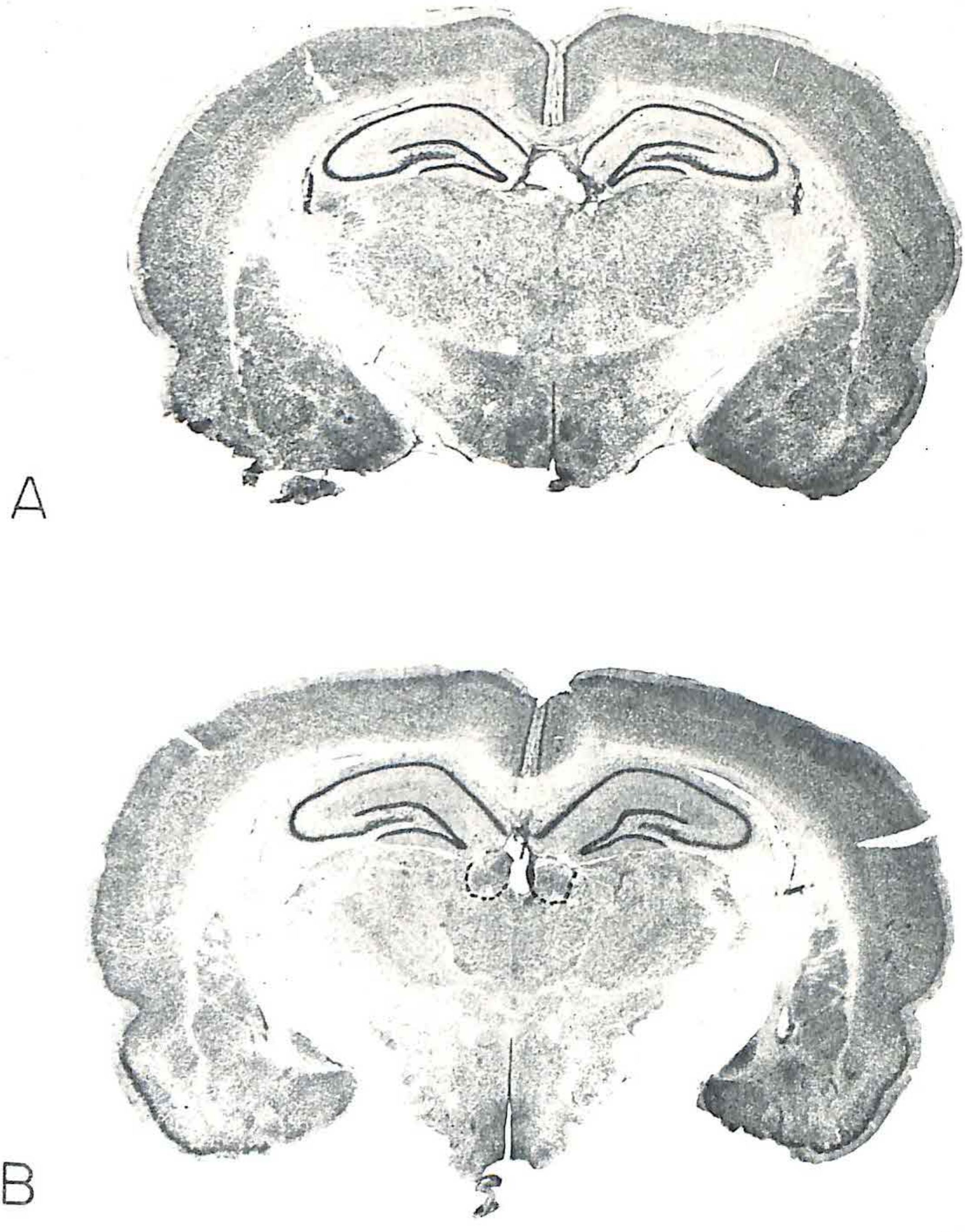

FIG. 2. Low-power photomicrographs of sections taken through the brains of two experimental animals with habenular lesions. *A*. Photograph taken through the greatest extent of the lesion in rat G 40 of Group II, showing complete bilateral destruction of the habenular complex. *B*. Photograph taken through the greatest extent of the lesion in rat G 39 of Group III, showing only minimal damage to the medial part of habenular nucleus on the right side. The lateral, medial, dorsal, and ventral extent of the habenular complex is indicated by broken lines in Section B.

behavior components including resistance to capture in home cage, resistance to handling, muscular tension, squealing, urination and defecation, and aggressive reaction to presentation and prodding with forceps. In addition, measurements of the magnitude of the startle reaction to an explosive auditory stimulus were made for all animals, utilizing a stabilimeter-like apparatus and procedure previously described in some detail (1).

Both emotional reactivity ratings and startle response measurements were taken for all animals on three occasions preoperatively (30, 15, and 1 day before surgery) and on five occasions postoperatively (1, 15, 30, 45, and 60 days after operation).

Operative and Histological Procedure

For the 12 animals in Group I with lesions in the septal forebrain area, the operative procedure was identical to that described in some detail in the previous report (1). Figure 1 shows a mid-sagittal and two frontal sections reconstructing the septal lesions in each of the 12 animals from this group. These lesions are similar both in extent and location to those reported for the operated septal animals in the previous experiment (1).

The habenular lesions in the ten animals of Groups II and III were produced electrolytically by the Horsley-Clark technique with a stereotaxic instrument similar in design to that described by Stellar and Krause (9). Placement of the lesions was accomplished with the aid of Krieg's coordinates for the brain of the albino rat, and in all other respects the anesthetic and surgical procedures were identical to those described for the previous experiment (1). As might well be expected, however, the extent of the lesions varied considerably in different animals, with the six rats in Group II showing rather extensive destruction of the habenula and the four rats in Group III showing only minimal involvement of this nuclear complex. Figure 2 shows photographic reproductions of sections through the greatest extent of the lesions in two animals typical of groups with maximal and minimal damage to the habenular nucleus, respectively.

Histological verification of the lesions was obtained for all 22 operated animals. Again, the details of the imbedding, cutting, staining, and reconstruction procedures were identical to those reported in some detail in the previous paper (1).

RESULTS

General Observations

In general, the 12 animals of Group I with septal lesions showed the same immediate gross and dramatic changes in emotional behavior found in the experimental septal groups of the previous experiment (1). Immediately following recovery from the anesthetic, an explosive wildness and fierceness developed in these animals which made them virtually impossible to handle without special precautions and which appeared to leave them hyper-reactive to all sensory stimulation, particularly tactual. A cinematographic record prepared in conjunction with the initial experiments illustrates quite clearly the character of these changes following septal lesions in the rat (2).

No such gross changes in behavior appeared, however, in any of the animals of Groups II or III with habenular lesions or in the unoperated control animals of Group IV. The postoperative behavior of these animals as observed under conditions of normal laboratory maintenance and care, transfer to and from the home cage and experimental apparatus, and the like, could not be distinguished from their preoperative performance, at least by such gross observational techniques.

Changes in the Conditioned Emotional Response

By the eighth conditioning trial all animals had acquired the conditioned emotional response. All 26 animals stopped pressing the lever during the clicker presentation, and 23 of the 26 animals defecated during the trial. No significant differences in rate of acquisition appeared, however, between the 6 animals of Group II operated (habenular lesions) prior to conditioning, and the remaining 20 animals of Groups I, III, and IV.

Complete retention of the conditioned emotional response was evident in all animals of Group II, Group III, and Group IV. All 14 animals stopped pressing the lever during the clicker presentation and defecated during the trial. In contrast, however, some reduction in the strength of the conditioned emotional response appeared in Group I on this first postoperative retention test. Of the 12 animals in this group, 6 (Fig. 1, rats 28, 54, 56, 65, 95, 105) showed at least partial attenuation of the CER (i.e., all 6 animals emitted some lever responses during the clicker presentation, and only one defecated). The remaining 6 animals (Fig. 1, rats 17, 37, 58, 59, 76, 93) retained a strong CER (i e., all 6 animals stopped pressing the lever during the clicker presentation, and 4 rats defecated).

Sixty days later, without intervening lever-pressing trials or clicker presentations, all 26 animals were again tested for retention of the CER, and a strong emotional response was evident in all rats, including the 6 animals of Group I which had shown immediate postoperative attenuation of the response. Furthermore, during the course of experimental extinction of the CER by nonreinforcement (presentation of the clicker alone without shock) during 11 successive daily trials following this second retention test, no differences between the animals in Group I were apparent.

Although the animals with habenular lesions

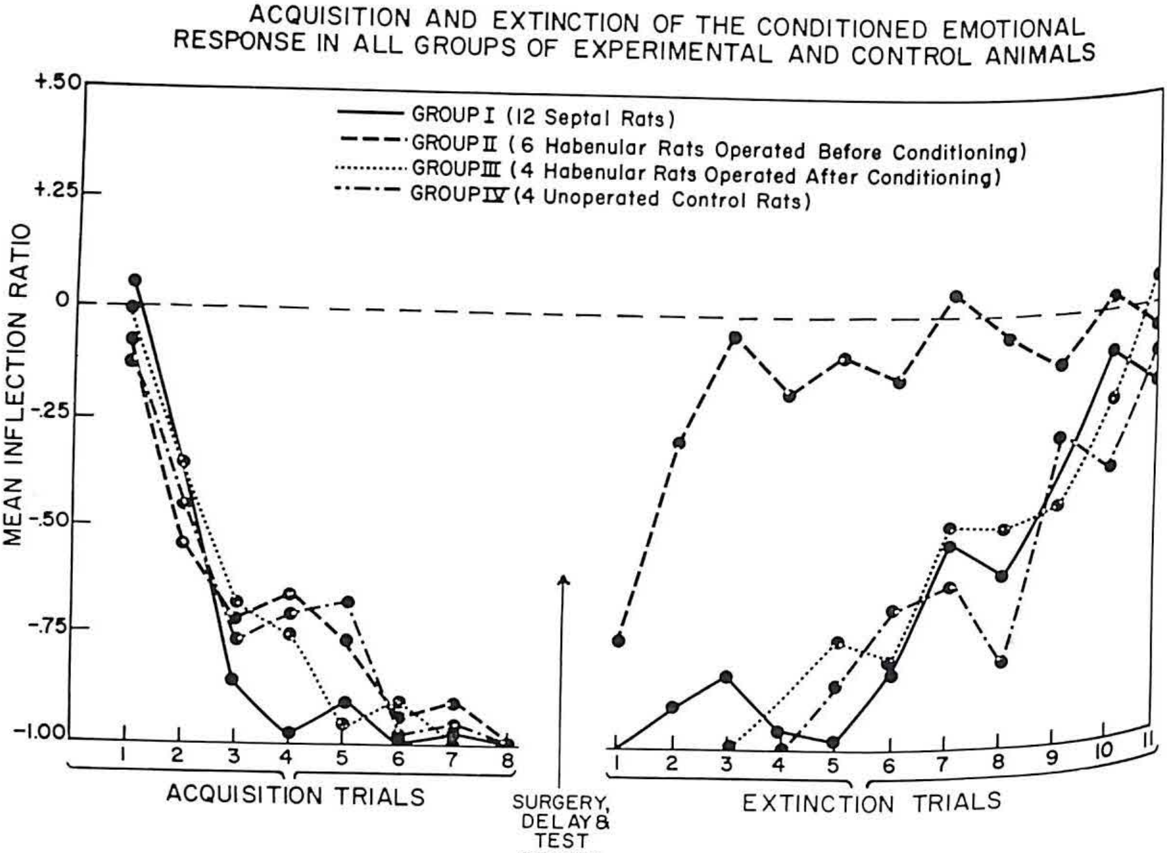

FIG. 3. Acquisition and extinction of the conditioned emotional response in all groups of experimental and control animals.

(Groups II and III) showed no apparent diminution in strength of the CER on either the first or second retention test, experimental extinction of the response was consistently more rapid in all 6 animals of Group II (operated prior to conditioning) than in either the 4 nonoperated controls (Group IV), the 12 septal animals (Group I), or even the 4 habenula animals operated following emotional conditioning (Group III). Figure 3 shows the average "inflection ratio" for each of the groups throughout the course of acquisition and extinction of the CER. The "inflection ratio" indicates how much and in which direction the clicker, during the second 3-min. of the trial, changes the output of lever responses (see reference 5 for a more complete discussion of the ratio). It expresses the difference in output between the first and second 3-min. segments of the curve as a fraction of the output during the first 3-min. segment. (The inflection ratio = $(B - A)/A$, where A is the number of lever responses made during the first, and B is the number made during the second, 3-min. segment of the curve.) Complete cessation of lever-pressing during the clicker (or second 3-min. of the curve) appears as a ratio of −1.00, essentially unchanged output appears as a ratio of around 0.00, and a 100 per cent increase in output appears as a ratio of +1.00.

As has been indicated, no differences appeared in rate of acquisition of the CER, the sharp drop toward −1.00 between the first and eighth conditioning trials reflecting the development of a strong response in all groups. The sharp rise in the curve for Group II between the first and third extinction trials, however, reflects the rapid weakening of the CER following nonreinforcement. In contrast, the curves for the other three groups show the retention of a strong CER well beyond the fifth or sixth nonreinforced extinction trial. By the third extinction trial, all 6 animals in Group II continued lever-pressing through the

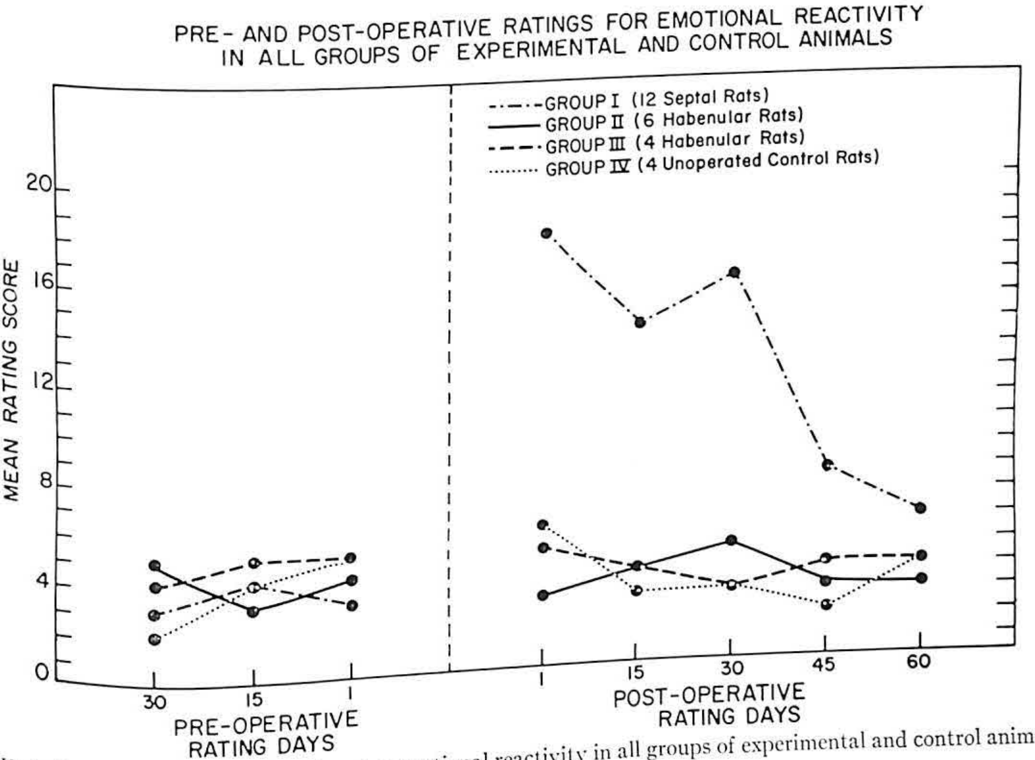

FIG. 4. Pre- and postoperative ratings for emotional reactivity in all groups of experimental and control animals.

3-min. clicker presentation and did not defecate. In contrast, of the remaining 20 animals, only 3 of the septal rats in Group I made any lever responses during this third extinction trial, and 16 of the 20 animals defecated in response to the clicker. This difference in frequency of defecation and incidence of lever responses during the clicker on the third extinction trial between the 6 animals of Group II, on the one hand, and all 20 animals in the other three groups, on the other, is highly significant (.01 level of confidence). Furthermore, the difference between the mean inflection ratios for Group II, on the one hand, and for the other three groups combined, on the other, throughout the course of extinction of the CER, as indicated in Figure 3, is highly significant (.01 level of confidence) by the Kruskal-Wallis rank-order test for the difference between uncorrelated means (6). The extensive operative involvement of the habenular nuclei in the animals of Group II (*A*, Fig. 2) produced prior to emotional conditioning appears to have markedly attenuated resistance to extinction of the conditioned emotional responses.

Changes in Emotional Reactivity and Startle Response

The results of the pre- and postoperative ratings for emotional reactivity in all four groups of animals are shown in Figure 4. It is apparent that no significant preoperative differences existed between the four groups. As in the previous experiment, however, there appeared a marked postoperative increase in the emotional reactivity of the experimental septal animals (Group I) as compared with both their own preoperative level and the level of the other three groups. The animals with habenular lesions (Groups II and III) showed no such change in emotional reactivity. The difference between each of the three preoperative ratings and each of the first three postoperative ratings for the animals of Group I is highly significant (.01 level of confidence). Furthermore, the difference between Group I on the one hand, and Groups II, III, and IV on the other, for each of the first three postoperative ratings is also significant beyond the .01 level of confidence. The figure also shows that the septal animals of Group I maintained this increased emotional reactivity virtually without abatement for a period of 30 days or more, with a rather abrupt decline in the magnitude of the ratings occurring between the thirtieth and forty-fifth postoperative day. This finding is in rather sharp contrast with the gradual decline in emotional reactivity during the 12-day postoperative rating period reported in the previous experiment (1).

The means of the startle responses in millimeters elicited on five trials conducted for each of the animals on each of the three preoperative and five postoperative test days were recorded for all four groups. Although there was no significant difference between the four groups on the preoperative tests, the septal animals of Group I again showed a marked postoperative increase in the magnitude of the startle response. None of the other three groups showed any such gross postoperative change in the amplitude of the startle response. The difference between the mean values for all three preoperative tests and the first postoperative test for the septal animals of Group I was highly significant (.01 level of confidence), as was the difference between the mean values on the first postoperative test for Septal Group I, on the one hand, and Groups II, III, and IV, on the other (.01 level of confidence). As in the case of the rated increases in emotional reactivity, however, a consistent and somewhat more rapid decline in the magnitude of the startle response was apparent in the septal animals of Group I on the four subsequent postoperative tests.

DISCUSSION

It is first of all clearly apparent that the results of these experiments tend to confirm, for the most part, the previously reported (1) changes in affective behavior following septal forebrain lesions in the albino rat. In addition, however, the present findings indicate that the immediate postoperative increases in emotional reactivity following septal lesions can decline markedly as a function of time alone. Within 60 days after operation, virtually all signs of such increased emotional reactivity had disappeared in the 12 septal animals of Group I (Fig. 4), even though they had been subjected only to minimal handling during the intervening period. Apparently, the rapid decline in emotional reactivity found in the earlier experiments (1) was a function more of the daily handling for rating purposes than the elapsed time of 12 days, although some interaction effects were undoubtedly operative.

The results of the present experiment also clarify somewhat the effect of such subcortical lesions upon the conditioned "fear" response as reported previously (1). First, the effects upon the conditioned emotional response appear to vary quite independently of the gross changes in emotional reactivity which follow septal lesions. Although virtually all the septal animals in Group I showed significant postoperative increases in rated emotional reactivity, only 6 of these 12 rats showed any quantifiable change in the strength of the conditioned emotional response, and, as in the previous experiment, such changes were apparently in the opposite direction (i.e., decreases in the strength of the CER) to the changes in emotional reactivity. Furthermore, inspection of the extent and location of the lesions in the animals of Group I suggests that postoperative attenuation of the CER may be related to the more extensive interruption of the fornix system and perhaps also to the slight involvement of the most rostrally situated thalamic nuclei in these 6 animals as compared with the 6 animals which showed complete retention of the CER (Fig. 1). No such relationships were discernible with respect to the magnitude of the changes either in rated emotional reactivity or startle response amplitude in the present group of septal animals.

The failure of any of the animals with habenular lesions to show increases in rated emotional reactivity or startle response magnitude makes it quite clear that the gross changes following septal lesions are not directly or solely related to interruption of the septal outflow to the habenular complex. The strong projection system from the septal region to the habenular nuclei via the stria medularis would, however, seem to implicate this nuclear complex as an integral part of the fornix system in its thus far ill-defined role as an important component of the neural substrate of affective behavior (3, 8). Indeed, the significantly more rapid extinction of the CER in Group II (habenular lesions placed prior to conditioning) would tend to suggest a possible functional relationship between those elements of the fornix system involved in the septal lesions which resulted in attenuation of the strength of the CER (Group I) and the habenular complex. It should be noted, in this connection, that such changes in the CER were not apparent in the animals of Group III (habenular lesions placed following conditioning) with less extensive involvement of the habenular complex [Fig. 2]).

Anatomically, the failure of the Group II and III animals to show the gross changes in emotional reactivity found in the Group I animals indicates that more important co-determinants of such reactive behavior are probably to be sought among the nonhabenular projections of the septal region (i.e., lateral hypothalamus, midbrain reticular formation [7]). In addition, the interruption of numerous hippocampal efferents among the fornix fibers involved in the Group I lesions would seem to suggest a further evaluation of the extent to which involvement of Ammon's horn and the dentate gyrus may be factorial in affective changes observed following septal lesions. A further investigation of these possibilities in an effort to elucidate the significance of individual components of the "rhinencephalon" for the integration of affective behavior is presently in progress and will be reported in a later paper.

SUMMARY

The present report describes a series of experiments investigating further the duration and specific character of behavioral changes in albino rats following lesions in the septal forebrain region and habenular complex of the thalamus.

Twenty-six male albino rats were divided into four groups. Group I (12 animals) received septal lesions, Groups II (6 animals) and III (4 animals) received habenular lesions at different stages in the experiments, and Group IV (4 animals) served as unoperated controls. Both pre- and postoperatively, data were collected on all animals with respect to (*a*) the acquisition, retention, and extinction of a conditioned emotional response (CER) of the "fear" or "anxiety" type, (*b*) the magnitude of the startle response, and (*c*) general emotional reactivity as reflected in a seven-item rating scale.

Upon completion of the behavioral observations, the animals were sacrificed and the lesions reconstructed histologically.

1. The results confirmed the previously reported postoperative increase in both emotional reactivity and startle response magnitude for the septal animals of Group I. No such effects were discernible in either the habenula animals (Groups II and III) or the unoperated control animals (Group IV). It is clear from the present findings, however, that such changes are of but limited duration, all animals returning to normal within 60 days after operation with only minimal intervening handling.

2. Six of the 12 septal animals in Group I showed at least partial attenuation in the strength of the CER on the first retention test within a few days after operation. Again, however, the reversible character of this reduction in the strength of the CER became evident during the second retention test some 60 days following operation, when all animals showed a strong emotional response. The temporary reduction in the strength of the CER appears to be related to the extent of involvement of the fornix system and anterior thalamic nuclei in the septal animals of Group I.

3. Although the habenular lesions produced no effect upon the acquisition or retention of the CER, extinction of the emotional response was significantly more rapid in the six habenula animals of Group II (operated prior to conditioning) when compared with all other animals. This effect would seem to be related to the extent of the damage to the habenular complex.

4. The relationship of these findings to recent neuroanatomical investigations of the fornix system has been discussed.

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AUDITORY FLUTTER FUSION IN PATIENTS WITH CORTICAL ABLATIONS

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It has been reported that fusion of intermittent light occurs at lower rates in man following lesions located in the frontal, parietal, and occipital lobes, and after diffuse brain injury. General agreement does not exist as to the magnitude and reliability of such shifts in the critical flicker frequency.

It would be advantageous both for the general goal of expanding our knowledge of cortical physiology and for the more immediate goal of providing quantitative behavioral indicators of cortical damage if it were possible to examine the effect of cortical lesions on fusion phenomena in other modalities. This possibility does exist in audition since white noise (a complex acoustic stimulus containing all audible frequencies at equal energy levels) may be rapidly interrupted to give rise to a sensation of flutter below a critical rate and to a sensation of continuous noise above the rate (5). Progress in the direction of improved instrumental and psychophysical approaches to the problem has made it possible to obtain auditory flutter-fusion (AFF) thresholds in naive subjects which may be compared with CFF values in the same individuals.

METHOD

Experimental Design

The problem to which the present study has been directed is the effect of a unilateral cortical lesion on the auditory flutter-fusion threshold. An ideal experimental design probably would include a combination of pre- and postoperative groups, one group which is tested for the first time after operation (to control learning factors), and appropriate controls (4). We have chosen a design which utilizes a comparison of matched operated and normal samples in the belief that the presence of an unknown degree of preoperative cerebral pathology places a severe restriction on the interpretation of data resulting from pre- and postoperative testing procedures alone.

The employment of this design necessitates careful selection of surgical material. Only patients with minimal neurological symptoms are acceptable, for the detection of general mental and physical deterioration is not the goal being sought; the intent is to examine a representative cross section of patients who are uncontaminated by variables not related to the specific pathology being studied.

Subjects

Operated group. The patient group was chosen on the basis of having a known surgical lesion situated exclusively in one of the major lobe subdivisions and being sufficiently free from intellectual or personality deterioration for cooperation and comprehension of the task. In addition, age limits between 12 and 55 years were set. A total of 41 such cases were seen and the AFF threshold taken as part of a battery of quantitative indicators. A description of this patient sample is given in Table 1. All but three cases were seen on an out-patient basis and are successfully rehabilitated into society. Most are regularly employed. The largest group consists of 21 unilateral and 2 bilateral anterior temporal lobe ablations done for the relief of psychomotor epilepsy (1). We are indebted to Dr. Percival Bailey (University of Illinois), Dr. John Green and the Arizona State Hospital (Phoenix), and Dr. Theodore Rasmussen (University of Chicago) for referring these cases to us for study.

Normal controls. The control sample was constructed in order to permit specification of the AFF threshold in a normal population with age and IQ comparable to the lesion group. From a series of 46 *S*s presenting no neurological complaints or history of significant head injury a group of 25 was chosen to form a matched sample. There is no significant difference between the mean AFF thresholds and standard deviations of this subgroup and the larger normal series reported elsewhere (9).

Procedure

The groups of normal and brain-damaged individuals described above were given a tape-recorded test developed in this laboratory which is designed to measure the fusion threshold for interrupted white noise. This test, which requires about 15 min. playing time, utilizes the principle of paired comparisons of continuous and interrupted noise. The *S* taking the test is instructed to listen for differences between the two bursts of noise in the pair to be compared, and to respond appropriately to each pair that is presented by writing the letter *S* for same or the letter *D* for different on an answer sheet. We have accepted as the definition of fusion that point in a rising scale of repetition rate (expressed in interruptions per second) beyond which interrupted noise is perceptually indistinguishable from continuous noise. In the repeated paired-comparison situation the fusion threshold is inferred from the occurrence of "same" responses.

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TABLE 1
Surgical Patients

Patient	Sex	Age	IQ	Reason for Surgery	Locus	Side	AFF (i.p.s.)
1	M	36	119	Epilepsy	Ant. Temporal	L	75
2	M	36	85	"	"	R	95
3	M	39	113	"	"	R	70
4*	M	33	99	"	"	L	70
5*	M	23	100	"	"	R	95
6*	F	12	82	"	"	L	75
7*	F	12	92	"	"	R	30
8	M	42	88	"	"	L	40
9*	F	18	92	"	"	R	70
10	M	54	91	"	"	L	50
11	M	39	70	"	"	L	35
12	M	36	67	"	"	R	30
13	M	38	84	"	"	R	50
14*	M	33	112	"	"	L	80
15	M	36	100	"	"	L	35
16*	F	22	115	"	"	L	60
17*	M	34	79	"	"	R	50
18*	M	30	119	"	"	Bilat.	45
19*	M	35	70	"	"	Bilat.	55
20*	M	32	99	"	"	L	60
21*	M	24	68	"	"	L	50
22	M	40	105	"	"	R	45
23	M	45	93	"	"	L	55
24*	M	23	122	Abscess	Frontal	R	80
25	F	48	94	Meningioma	"	R	50
26*	M	22	99	Cyst	"	R	35
27	M	36	102	Meningioma	"	L	45
28*	F	35	64	Glioma	"	R	30
29*	M	15	75	Glioma	"	L	45
30*	M	30	104	Abscess	"	R	40
31	F	46	104	Aneurism	"	R	85
32*	M	31	88	Abscess	"	R	40
33*	M	35	116	Parkinsonism	"	L	70
34*	M	16	—	Glioma	"	L	55
35*	M	31	85	Epilepsy	Parietal	R	40
36*	M	18	—	Epilepsy	"	L	55
37*	F	24	91	Glioma	"	L	40
38	F	49	74	Hematoma†	"	L	30
39*	M	30	79	Angioma	"	L	45
40	M	37	75	Epilepsy	"	L	65
41*	F	13	137	Glioma	Occipital	R	45

* Less than 36 years of age. † Considered as tumor in Table 4.

The test consists of 60 pairs of noise bursts, the first always continuous and the second always interrupted, covering the range of repetition rates from 10 to 150 interruptions per second (i.p.s.) in 10-i.p.s. steps. Each repetition rate appears four times in all. It has been determined that this range will include the fusion threshold for 99 per cent of the testable population under standard conditions of .90 sound-time fraction and 70 db. re .0002 dyne/cm² sound pressure level. The sound pressure level refers to that generated by a burst of continuous noise in a rigid 6-cc. coupler. The interrupted noise is equated for loudness to this standard. Standardization of the temporal programing of the stimuli is achieved through the use of a high quality tape playback machine, and intensity control is obtained by calibrating the output of the playback machine into high fidelity earphones (Permoflux PDR-8). All threshold testing reported here has been done binaurally.

A practice column of eight pairs and detailed instructions are recorded on the tape, and it has been observed that all the normals and some of the patient group can take the test satisfactorily on the basis of these instructions alone. Many patients, however, require additional verbal instructions, or repeated playings of the recorded instructions. These have been given freely where needed, in the belief that the principle of the test (the discrimination of differences between bursts of sound) must be understood clearly by all who take it and that the difficulty of acquiring such understanding is not directly relevant to the problem under consideration.

In scoring the test a key is consulted giving the repetition rate corresponding to every S response on the answer sheet. The number of failures at each repetition rate is tabulated in a space provided on the answer sheet, and the typical result is to observe few or no failures at the lowest rates, a range of uncertainty in which about half the presentations are missed, and a suprafusional range where most or all are missed. The convention has been adopted of taking as the fusion threshold the mid-point of the interval of uncertainty, which is estimated to the nearest multiple of 5. This corresponds with the psychophysical notion of a threshold as that stimulus cue which is responded to 50 per cent of the time. In those cases where no satisfactory 50 per cent point could be estimated (less than 5 per cent of the total), the test was discarded as not meaningful in our present concept of flutter fusion.

RESULTS

From the 41 cases of cortical lesion tested those of age less than 36 years were selected to form a comparison sample (the 25 cases bearing asterisks in Table 1). The younger group was chosen to minimize the factor of general deterioration in our patient sample. This sample is matched by the control group described previously. The mean values for age, IQ, and AFF score for both groups are displayed in Table 2. The statistical significance of the difference between the mean AFF scores is greater than the .0001 level of confidence, considered both parametrically and nonparametrically. A correlation (Pearson *r*) of .161 between IQ and AFF was obtained based on 32 control *S*s, which compares with a value of .041 based on 39 operated cases.

It is essential to determine whether the observed difference in mean scores implies a lowered threshold in the operated group (as reflected in poorer discrimination at all repetition rates) or simply a greater error score on a complex task. In Figure 1 the per cent frequency with which interrupted noise is discriminated from continuous noise is plotted as a function of repetition rate for both the larger series of operated and control *S*s. The number of D responses divided by the sum of S and D responses for the entire group is the per cent scale on the ordinate. The dashed line in Figure 1 indicates the per cent frequency with which identical bursts of continuous noise are judged "different" by normal *S*s when such discriminations are interspersed with difficult (more than 50 per cent missed) continuous vs. interrupted discriminations. This mock discrimination level was determined independently in 109 normal *S*s on an earlier form of the test.

TABLE 2
Operated and Normal Samples

	N	Age	IQ	AFF	SD
Operated	25	25.2	94.9	54.4	17.0
Normal	25	23.1	94.0	80.0	17.2

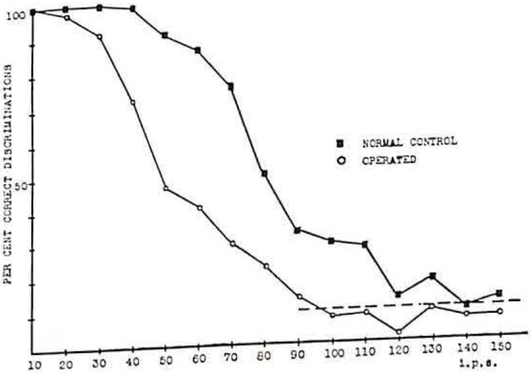

FIG. 1. Per cent frequency with which interrupted noise is discriminated from continuous noise as a function of repetition rate. The sound–time fraction is .90 and the sound pressure level is 70 db. re .0002 dyne/cm².

The shape of the functions plotted in Figure 1 suggests that there is a lowered discriminatory capacity in the operated group throughout the range where performance is at other than a chance level. The excellent correspondence of the repetition rates at the 50 per cent point (true group threshold) with the means of individual scores argues that the method of assigning individual thresholds is not producing spurious information.

The relationship between locus of lesion and degree of impairment on this indicator may be examined by comparison of mean scores for the several subgroups selected on the basis of the lobe in which the lesion occurs. Table 3 gives the mean AFF scores for frontal, temporal, parietal, occipital, and all right-sided and all left-sided lesions. This analysis fails to reveal significant differences among the various subgroups.

Table 4 indicates that the group operated for tumors of various kinds is significantly lower in AFF threshold than the groups operated for other reasons. The *t* value based on this difference between means could occur by chance about five times in a hundred such

TABLE 3

Performance by Locus of Lesion

Measure	Fron.	Temp.	Par.	Occ.	Rt. Side	Lft. Side
N	11	23	6	1	18	21
Mean AFF	52.3	57.4	45.8	45.0	54.4	54.0
SD	18.4	18.8	12.4	—	22.2	14.6

TABLE 4

Performance by Reason for Surgery

	Epilepsy	Tumor	Other
N	26	9	6
Mean AFF	56.9	42.8	58.3
SD	18.1	8.3	22.5

samples, indicating a fair degree of certainty. This difference cannot be attributed to the gross extent of lesion as visualized at time of surgery.

The fact that many of our control and operated *S*s were given a test of visual flicker fusion immediately prior to or immediately following the AFF test has presented an opportunity for obtaining a correlation between the two sets of scores which minimizes the effects of day-to-day variability. The apparatus used for obtaining CFF thresholds has been described by Halstead (3). A Pearson correlation coefficient of .43 (.01 level = .45) was observed in a sample of 32 normal individuals between the ages of 20 and 45 years.

DISCUSSION

It seems reasonable to conclude from our results that a difference exists between the normal and the operated groups on a particular test of AFF threshold in the direction of poorer performance in the latter group.

One variable in which the two samples were not explicitly matched and which must be considered in an attempt to classify the variance is the audiometric acuity of the operated group. Two points argue that high- or low-tone hearing losses are not a sufficient explanation of the observed AFF threshold difference. First, the incidence of abnormal pitch thresholds is low in the types of surgical cases we have seen. Even in the temporal lobe group it is probably not greater than that in the normal population (2). Second, it appears on the basis of preliminary information that the AFF threshold is independent of pitch thresholds as long as some part of the audiometric range is intact. Thus neither high- nor low-tone loss is sufficient to produce by itself a lowered AFF threshold, although a severe loss over the entire range is.

For a further analysis of the possible causes for the observed difference in mean scores we must turn to a hypothesis regarding the mechanism of auditory flutter fusion which has received some experimental support. It is assumed that the cue for the perception of flutter is a just detectable change in loudness of the noise. In other words, at the point of fusion the off interval in the interrupted noise is just equal to the time required for the auditory perception to decay one detectable step (intensity jnd), and the cue for flutter is heard about half the time. Two physiological parameters are thus implicated: the rate of decay of the physiological correlate of loudness, and the minimum unit of physiological change which reaches the threshold of perception. Both these parameters of auditory perception have been measured experimentally, and predictions as to the point of fusion based on values thus obtained have been in remarkable agreement with observed fusion points for the conditions of intensity and sound-time fraction employed in the present test (8, 9).

In the absence of compelling evidence at the present time it seems reasonable to raise the hypothesis that an increase in the minimal perceptible unit of change (jnd) is a causal factor in our results. The most attractive explanation of the rate of decay of an auditory perception at a given intensity is that it is related to the difference in conduction rate between the fastest and slowest fibers responding in the afferent complex (7). That a cortical ablation would affect this difference (making it greater) seems unlikely from present evidence.

The observed shift in the average threshold can be satisfactorily explained if the single assumption is made that the difference limen for intensity of noise is raised from .4 db. in normals (6) to .6 db. in the operated cases. Such a change in the sensitivity of the listener would have the effect of reducing the AFF threshold by a factor of 2/3, which would in turn generate a new distribution with a mean

2/3 as large as the mean of the first and a standard deviation of similar relative size. Our sample values are sufficiently close to these predictions to allow us to accept provisionally the hypothesis that the distribution of operated scores is derived from the control distribution as a result of a rather small shift in the magnitude of the jnd. From the standpoint of consistency with the suggested mechanism for flutter fusion outlined above it is not necessary to invoke a gross change in the differential sensitivity of the organism. This may be an illustration of a minimal deficit resulting from unilateral cortical damage, which is exposed by the use of a quantitative threshold indicator.

SUMMARY

1. A method for rapidly determining the fusion threshold for interrupted white noise (expressed as interruptions per second) in naive and brain-injured patients is described.

2. A coefficient of correlation of .43 has been obtained between successive measurements of visual flicker fusion and auditory flutter fusion in 32 normal individuals.

3. A lowered auditory flutter-fusion threshold has been found in patients with unilateral surgical ablations of cerebral cortical tissue.

4. The degree of impairment on this test appears to be constant for the several loci of cortical lesion studied.

5. A hypothesis is advanced that the cause of the lowered fusion threshold is a minimal loss in differential sensitivity to intensity of white noise.

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BINAURAL INTERACTION AT THE INFERIOR COLLICULI[1]

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The localization of sounds in space has recently been correlated with functional properties of the responses of the auditory cortex (3, 9). At the same time it should be recognized that auditory localization is not totally dependent upon the auditory cortex. Bard and Rioch (2) noted that decorticate cats could localize sounds in a free situation; the accuracy of localization was not measured. Girden (6) trained dogs to flex the forepaw when a sound came from the right side but to inhibit the response when a sound came from the left. Complete bilateral extirpation of the auditory cortex abolished the learned response, but the animals still oriented their heads to the sounds. Neff, Arnott, and Fisher (8) found that whereas normal cats were able to discriminate a difference of 5° in the direction of sound sources, this threshold rose to 40° after bilateral extirpation of the auditory cortex. The discrimination behavior was no longer stable after the operation; it fluctuated between chance and 100 per cent on successive days. Apparently the auditory cortex is important in the control of trained responses to the location of the stimulus, but some localization can be accomplished in the absence of the auditory cortex.

A few studies have sought indications of binaural interaction in the electrophysiological responses of subcortical auditory centers. Tunturi (10) found the same binaural interaction at the medial geniculate body (the auditory center of the thalamus) that he had found at the cortex. However, the medial geniculate cannot be responsible for localization in the absence of the cortex, since it degenerates when the cortex is extirpated. The impulses entering the medial geniculate from lower levels of the auditory system gave some evidence of binaural interaction. Recording at the brainstem, Kemp and Robinson (7) interpreted their results to mean that there probably is no binaural interaction at the lateral lemniscus. A preliminary report has indicated evidence of binaural interaction in the earliest neural response recorded at the cochlea (5), but this has not been confirmed.

We have undertaken the present study in order to determine whether impulses from the two ears interact in the midbrain auditory centers, the inferior colliculi. By "binaural interaction" we mean that the responses of the two ears affect each other and do not simply add together algebraically. More precisely, interaction will be said to be demonstrated if the response to stimulation of both ears, the stimuli being either simultaneous or successive, differs from the sum of the responses of the two ears to monaural stimulation.

METHOD

Electrophysiological responses were recorded at the midbrain of anesthetized cats. The amplified responses were photographed from a cathode-ray oscilloscope.

Stimulus equipment. (*a*) Pulse generator (Grason-Stadler). The generator produces electrical square waves of 0.3 msec. duration. Time interval between paired stimuli was varied from 0 to 100 msec. We will refer to the interval between paired stimuli as the "delta interval." Intensity of the pulses could be varied in 1-db steps. (*b*) Two PDR-10 (Permoflux) earphones, one for each ear. The earphones were matched for response and for polarity. (*c*) Coupling from earphones to ears—flexible plastic tubes, 0.4 cm. inner diameter, 6 cm. long; from special housing on earphone into incision in external auditory meatus.

Recording equipment. (*a*) Gross electrodes—silver wire. (*b*) Dual channel amplifier (Grason-Stadler). Response components below 20 cps and above 1000 cps were filtered out. (*c*) Dual channel cathode-ray oscilloscope (Electronic Tube Corp.). (*d*) Oscilloscope motion picture camera (Grass Kymograph Camera).

Measurement of responses. Film is placed in microfilm reader, and enlarged image is plotted on grid.

Physiological preparation. Twelve adult cats were used. The animals were anesthetized with Dial in urethane. The calvarium was exposed and opened over the cerebellum. The cerebellum was removed by aspiration, revealing the fourth ventricle and the inferior colliculi. The electrodes were placed approximately on the center of the caudal surface of each colliculus. The animal was usually kept alive for a full day of experimentation; the date of the experiment is given on each figure.

RESULTS

Figure 1 shows oscillograms of responses recorded at the inferior colliculi. The responses in squares *1* and *2* were recorded simultane-

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[1] An abbreviated version of this paper was presented at the 1954 meeting of the American Psychological Association, New York, N. Y.

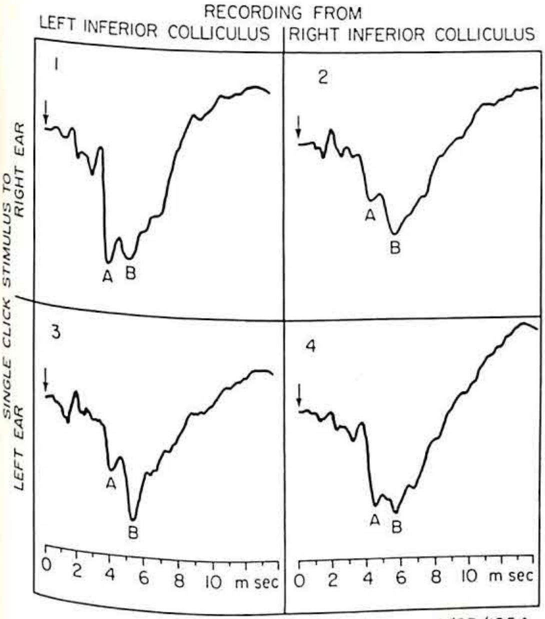

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FIG. 1. Oscillograms of electrophysiological responses of the inferior colliculi to monaural click stimuli. The responses are described in the text.

ously at the left and right inferior colliculi, respectively, when a click stimulus was delivered to the right ear. Responses *3* and *4* were recorded simultaneously when a click was delivered to the left ear. The arrow at the start (the left) of each trace indicates the time of arrival of the electrical pulse at the earphone. A downward deflection indicates a surface-positive response at the electrode. In square *1* (left colliculus response to stimulation of the right ear) delivery of the stimulus is followed shortly by some wavelets reflecting activity of levels lower than the colliculus in the afferent auditory system. Then at about 4 msec. there is a large surface-positive deflection labeled *A*. It is followed closely by another deflection, *B*, whose peak occurs a little more than 5 msec. after the stimulus.[2] There is a suggestion of another peak, and then there is a negative deflection whose full duration is not shown in the figure. The negative deflection may last 20 msec. or more. The amplitude of the collicular response may reach several hundred microvolts. The stimulus in this case was intense about 100 db above threshold. The amplitude would be smaller and the latency greater for responses to weaker stimuli. In square *2* (right colliculus response to stimulation of the right ear) the response occurs in the colliculus ipsilateral to the ear stimulated. The response is similar to that in square *1*, but there are characteristic differences: deflection *A* in this ipsilateral response is clearly smaller than deflection *B*, and both deflections are smaller than the corresponding ones in the contralateral response of square *1*. The responses to stimulation of the left ear in squares *3* and *4* show similar differences, with deflection *A* being relatively smaller in the ipsilateral response of square *3*. Here deflection *B* in square *3* is not smaller than *B* in the contralateral response of *4*, an exception to our general observation. Note that the response of square *2* resembles that of square *3*, though *2* involves the right ear and right colliculus while *3* involves the left ear and left colliculus; both are ipsilateral responses. Similarly the two contralateral responses, *1* and *4*, are rather alike. (Other contralateral responses are shown in Figure 2, square *2*, and in Figure 5, square *1*; other ipsilateral responses are in Figure 2, square *1*, Figure 3, and Figure 5, square *3*, the last being an atypical case.) We conclude that the form of the collicular response and the relation between the responses of the two colliculi give information as to which of the two ears was stimulated.

The fact that each colliculus responds to stimulation of either ear does not in itself indicate that binaural interaction occurs at this level. We could explain this fact by hypothesizing that the two ears are represented at the colliculus by neighboring but independent populations of neural units. One test for binaural interaction can be made by stimulating the ears singly and then simultaneously. If the two ears are represented by independent populations, then the amplitude of the response to simultaneous stimulation should equal the sum of the responses of the right and left ear to monaural stimulation. (This test is crucial only for relatively weak stimuli, since a stimulus more than about 40 db above threshold may leak from one ear to the other, arriving at the far ear with enough intensity to elicit a response.) Table 1 presents data obtained when this test was conducted on one animal. It is clear that the responses to simultaneous stimulation (SS) tend to be

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[2] Deflection *A* presumably represents the activity of third-order neurons of the auditory system; deflection *B* presumably represents fourth-order neurons.

TABLE 1

Response Amplitude versus Stimulus Intensity in Decibels above Threshold; Monaural and Binaural Stimuli

	Deflection A of Collicular Response				Deflection B of Collicular Response			
	10	20	30	40 db	10	20	30	40 db
L	8	15	27	32	7	11	21	26
R	2	10	15	20	3	13	20	29
L + R	10	25	42	52	10	24	41	55
SS	9	22	32	41	10	19	33	36

L indicates monaural stimulation of the left ear. *R* indicates monaural stimulation of the right ear. *L* + *R* was obtained by adding the L and R values. *SS* indicates simultaneous stimulation of the two ears. Amplitude is given in arbitrary units. Each value is the median of five responses. The responses were recorded at the right inferior colliculus. Experiment of 5/21/1954.

smaller than the sum (L + R) of monaural responses of the two ears. This difference is small or nonexistent at 10 db above threshold. In fact, for deflection *B*, SS is sometimes larger than L + R at this intensity level. But by 30 or 40 db above threshold, SS is falling behind L + R by increasing amounts. The difference between SS and L + R tends to be greater for deflection *B* than for deflection *A*. This test was also conducted on the other colliculus of this animal and on both colliculi of three other animals, in all cases with similar results. The results may be interpreted as indicating that the two ears are represented at the colliculi by neural populations that overlap in part.

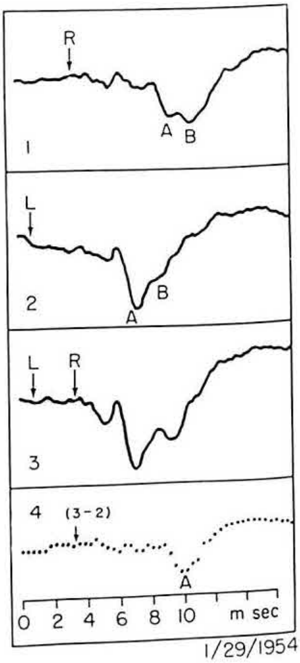

FIG. 2. Testing for binaural interaction with successive stimuli. Oscillograms recorded at the right inferior colliculus. *1*. Response to monaural stimulation of the right ear. *2*. Response to monaural stimulation of left ear. *3*. Response to paired stimuli, the one to the left ear preceding the one to the right ear by 2.8 msec. *4*. Graph obtained by subtracting responses obtained under condition *2* from responses obtained under condition *3*. The graph shows that the response to the second stimulus has been modified by binaural interaction.

The existence of binaural interaction can also be tested by the use of successive stimuli, as Figure 2 demonstrates. The apparatus was set so that the right stimulus was delivered 3.5 msec. after the start of the trace, and the left stimulus, 0.7 msec. after the start of the trace. The stimuli were only 40 db above threshold to avoid leakage of stimuli from one ear to the other. The responses were recorded at the right colliculus. Square *1* shows the response to the right-ear stimulus; square *2* to the left stimulus. The response shown in *3* resulted when both stimuli were delivered with the 2.8-msec. interval between them. If response *1* and response *2* occurred in separate populations of neural units, response *3* would be the sum of *1* and *2*. To test this, we subtracted response *2* from response *3*. (More accurately, we measured the amplitude of responses every 0.3 msec. along the trace. Then we took the median of five responses obtained under condition 2 and of five responses obtained under condition 3 and found the difference between these medians at each point along the trace.) Subtraction yielded the unimodal response shown in square *4*. The peak of this response is slightly lower and later than that of deflection *A* in square *1*. Deflection *B* has vanished. Thus the response to the second stimulus has been modified by the effect of the first stimulus—further proof of binaural interaction at the colliculus.

It may be asked why the single peak of the modified response in Figure 2 is identified with deflection *A* and not with deflection *B*. The answer can be found in Figure 3, which shows modified responses obtained at several delta intervals (time intervals between paired stimuli). Each of these modified responses shows a deflection which corresponds closely in latency with deflection *A* of the normal response. The

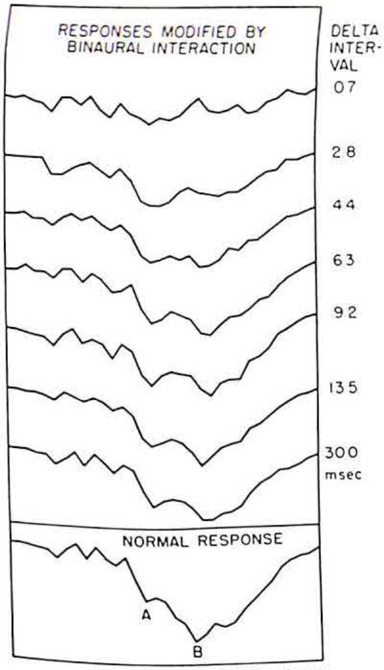

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Fig. 3. Graphs of responses modified by binaural interaction compared with a graph of a normal response. All the responses were recorded at the right colliculus and were evoked by equal clicks to the right ear. In each case but that of the normal response, a click to the left ear preceded the click to the right ear. As the interval between paired clicks (the delta interval) becomes longer, the modified responses resemble more closely the normal response. Five to seven responses were measured for each condition.

modified responses at the top of the figure show little or no second peak. As the delta interval is increased, the responses show a second deflection, which grows steadily to resemble deflection *B* of the normal response.

Similar progressive changes are presented graphically in Figure 4, the data coming from another animal with which more of the shorter delta intervals were employed. In graph *A* we have plotted the amplitude of deflection *A* of the modified responses versus the delta interval. Even at 0.4 msec., the shortest delta interval shown, the amplitude of deflection *A* was reduced by only one-third. When the delta interval was increased to 3 or 4 msec., this deflection was back to its normal size. The height of the horizontal section of the graph was taken from the amplitude of normal control responses. In general, deflection *A* is not strongly modified in contralateral responses, of which this is an example. In ipsilateral responses the smaller deflection *A* may be reduced by binaural interaction to one-third of its normal amplitude. In graph *B* we have plotted deflection *B* of the modified responses. At the shortest delta intervals the amplitude is reduced to about one-tenth of normal. There is a relatively large discontinuity in this case between 1 and 2 msec. Then the graph rises in roughly linear manner on this semilogarithmic plot. The normal level is attained only at a delta interval of about 20 msec. We have obtained similar data for modified responses of the right and left ear at both colliculi of four animals, and we have tested other animals at a few delta intervals. The form of the graph varies somewhat from animal to animal and even between the two colliculi of a single animal. But in each case deflection *A* has recovered its amplitude completely within about 4 msec., while *B* takes at least 20 msec. to recover, and in most cases the maximum effect is greater in *B* than in *A*.

In addition to varying the delta interval, we varied the intensities of the stimuli in several experiments. Other things being equal, the more intense the first stimulus, the greater the modification of the response to the second

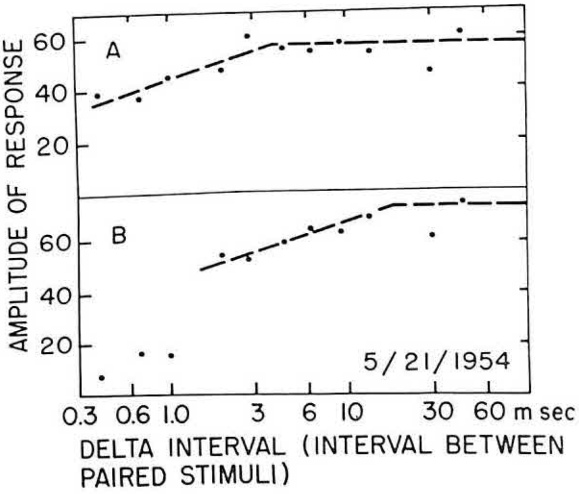

Fig. 4. Response amplitude versus delta interval. (The time scale is logarithmic in order to accommodate both short and long delta intervals.) Graph *A*: Amplitude of deflection *A* of collicular responses. Graph *B*: Amplitude of deflection *B* of the same collicular responses. Note that *A* regains normal amplitude (the horizontal section of the graph) at a delta interval of about 4 msec., whereas *B* regains normal amplitude only at about 20 msec.

stimulus. We also presented both stimuli to the same ear in some experiments. Generally, the effects of monaural interaction were greater than those of binaural interaction. The results obtained with variation of stimulus intensity and with monaural stimulation will be described in detail in a separate publication.

The rather heavy commissure running between the two colliculi has been suggested as having possible significance in localization (1). Accordingly, we sought to determine whether the commissure is required for binaural interaction to occur at the colliculi. We interrupted the commissure in six animals, in some cases transecting it and in other cases removing it by aspiration. We used successive clicks to test for binaural interaction before and after interrupting the commissure. The normal responses were altered somewhat when the commissure was interrupted, both because the electrodes could not be repositioned exactly and because the volume of responding tissue was changed. Therefore, the modified response should be compared in each case with its control normal response. It is clear in Figure 5 that responses *6* and *8*, obtained after the commissure was cut, are modified from the corresponding normal responses, *5* and *7*. Moreover, *6* and *8* are not greatly unlike the modified responses *2* and *4* obtained while the commissure was intact. Similar results were obtained with the other animals. Evidently the commissure is not required for binaural interaction to occur at the inferior colliculi.

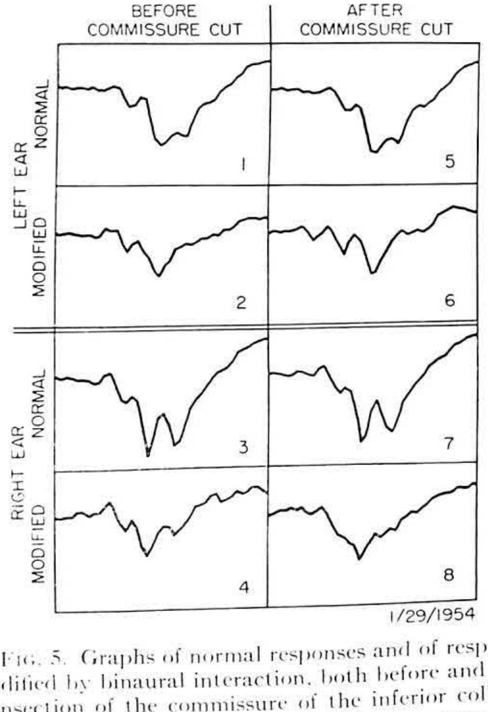

FIG. 5. Graphs of normal responses and of responses modified by binaural interaction, both before and after transection of the commissure of the inferior colliculi. The delta interval was 1.0 msec. The responses were recorded at the right inferior colliculus. Normal responses *1* and *5* and modified responses *2* and *6* were evoked by stimulation of the left ear; normal responses *3* and *7* and modified responses *4* and *8*, by stimulation of the right ear.

DISCUSSION

Our description of the responses of the colliculi differs in two important respects from that of Ades and Brookhart (1). They state, "Difference in latency of response of inferior colliculus to ipsilateral and contralateral stimulation plus difference in the earliest peak or shoulder of the collicular and brachial responses indicate one more synapse in the ipsilateral pathway than in the contralateral" (p. 204). They report that the earliest peak or shoulder (which we have labeled deflection *A*) is diminished or *absent* in the ipsilateral responses. We have not observed a case of absence of *A* in the ipsilateral response. The published records of Ades and Brookhart (their Fig. 3) all seem to show at least a trace of *A* in the ipsilateral response, and in some cases it is rather large. Furthermore, we have not observed much difference in the latency of ipsilateral and contralateral responses. Ades and Brookhart used the first positive swing of the base line to estimate latency "grossly, but significantly." We used the latency of the peak of the deflection for two reasons: (*a*) It is more reliable inasmuch as it is less apt to be confused with fluctuations of the base line. (*b*) The peak latency seems to be the more representative measure because it is, in a sense, the mode in the latency spectrum of the population of responding neural units. Thus, we do not find evidence in our observations for the conclusion that there is one more synapse in the ipsilateral pathway than in the contralateral.

After completing our study, we learned of the recent unpublished thesis of Coleman in which binaural interaction at the inferior colliculus was investigated (4). It is somewhat difficult to make detailed comparisons between his results and ours, since Coleman used only three delta intervals—10, 20, and 50 msec.

Also, Coleman observed the responses with an oscilloscopic sweep speed only about one-fifteenth as fast as ours; consequently, he could not distinguish the different positive deflections in the collicular response. His measurements of amplitude were made from the base line to "the peak" of the response. Probably these measures were chiefly of deflection *B*, although the amplitude of deflection *A* probably set a minimum to the measures of modified responses at these delta intervals. Coleman interpreted his results as demonstrating that binaural interaction does occur at the inferior colliculus. In addition, we are in agreement with his two further general conclusions: "(1) increasing the intensity of the first click leads to greater inhibition of the response to the second click, (2) decreasing the duration of the interval between clicks leads to greater inhibition of the response to the second click" (4, p. 172).

SUMMARY

Although cortical correlates for the localization of sound in space have been demonstrated, it is clear that some ability to localize sounds is possible in the absence of the cortex. Therefore, we recorded electrophysiological responses at the inferior colliculi in order to determine whether impulses from the two ears interact at this level of the auditory system. Click stimuli were delivered independently to the two ears. At both the left and the right inferior colliculus, responses to stimulation of the ipsilateral and contralateral ear showed characteristic differences in amplitude and wave form. Evidence for binaural interaction was found in the following observations: (*a*) The response to simultaneous stimulation of the two ears is smaller in amplitude than the sum of the responses to monaural stimulation of each ear. (*b*) When one ear is stimulated slightly before the other, the response to the second stimulus is modified. Of the two main surface-positive deflections of the collicular response, the first can be modified by binaural interaction only when the interval between paired clicks is less than about 4 msec. The second deflection can be modified up to intervals of about 20 msec. The maximum extent of modification is greater for the second deflection than for the first.

Severing the commissure of the inferior colliculi does not abolish the binaural interaction.

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EFFECT OF CORTICAL IMPLANTATION OF RADIOACTIVE COBALT ON LEARNED BEHAVIOR OF RHESUS MONKEYS[1]

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The discrepancy between the behavioral effects of active and presumably irritative pathological brain processes and the effects of surgically produced lesions involving equal or greater areas has long been a puzzle to observers. Much experimental literature exists on the effects of surgically produced lesions, but no one has reported the successful production of irritative lesions radically influencing learned behaviors. On the possibility that such lesions might be produced through the implantation of radioactive materials, a series of preliminary studies was undertaken to investigate the behavioral effects of cortical lesions produced by cobalt 60. In 1933, one of the authors reported a study (1) in which radon seeds were implanted in the cortex of monkeys, but inconclusive results were obtained because of the insensitivity of the behavioral tests employed and the loss of the animals through disease before the experiment was completed.

METHOD

Subjects

Two male rhesus monkeys, no. 167 and no. 212, were used in this original exploratory investigation. The former animal had been extensively tested over a two-year period and had received intensive training on delayed response. Monkey 212 had been tamed and tested for more than six months, but was less stable and a less effective performer than monkey 167. Throughout its laboratory history, *S* 212 was difficult to motivate for testing. Animal 167 weighed 7.1 kg., and animal 212, 3.3 kg., at the beginning of the experiment.

Apparatus

The Wisconsin General Test Apparatus (2) was employed throughout. Stimuli were those standardized for the particular situations described.

General Procedure

The general test procedures were previously standardized at the Wisconsin laboratory. Individual test procedures are indicated separately in the presentation of the experiments which follow. The method of producing the cortical lesions by cobalt 60 implantation was described in an earlier paper by Settlage and Bogumill (5). The sites of the sources of all lesions in monkey 167 are indicated in Figure 1.

EXPERIMENT 1. EFFECT OF BILATERAL PREFRONTAL COBALT 60 IMPLANTATION ON DELAYED-RESPONSE PERFORMANCE

Method

Monkey 167 served as *S*. Because of its previous extensive delayed-response experience, preoperative training was limited to a single session of 40 trials, 10 each at 0, 5, 10, and 20 sec. of delay. Half the trials were presented with the forward opaque screen up, and half with the screen down. Each delay interval was continued for 5 successive trials, the order of intervals being determined from a latin square. The same procedure was employed during the first 8 postoperative test days. For the next 20 days, *S* was given 20, 10-sec. delayed-response trials, half with the forward screen up, half with it down. Following delayed-response testing on each of these 20 days, *S* was given 20 discrimination trials—2 on each of 10 problems—in an attempt to determine the feasibility of broadening the battery. Two-trial discrimination procedures and scoring have been described previously (3).

The cobalt 60 was applied bilaterally in one treatment to the frontal areas with the tips of the needles 5 mm. below the surface of the cortex and the cobalt source at the cortical surface. The dosage at each site was 8000 r. calculated at a distance of 5 mm. from the center of the source of radiation.

Results

Performance of *S* on delayed response on the preliminary test day and during the postradiation period is summarized in Figure 2. It is obvious that following cortical irradiation, performance on delayed-response tests was temporarily at a low level. Progressive recovery of performance started after the fourth or fifth postoperative day.

The protocols of general behavior show that 167 was easily distracted in the test situation on the first day and inattentive and lethargic on the next three days. During days 5 and 6 the monkey was found prostrate in the home cage, and it was presumed that death would shortly ensue. But on both days the animal

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[1] These researches were supported in part by a grant to the University of Wisconsin from the Atomic Energy Commission Contract AT(11-1)-64 and in part by the Research Committee of the Graduate School from funds supplied by the Wisconsin Alumni Research Foundation.

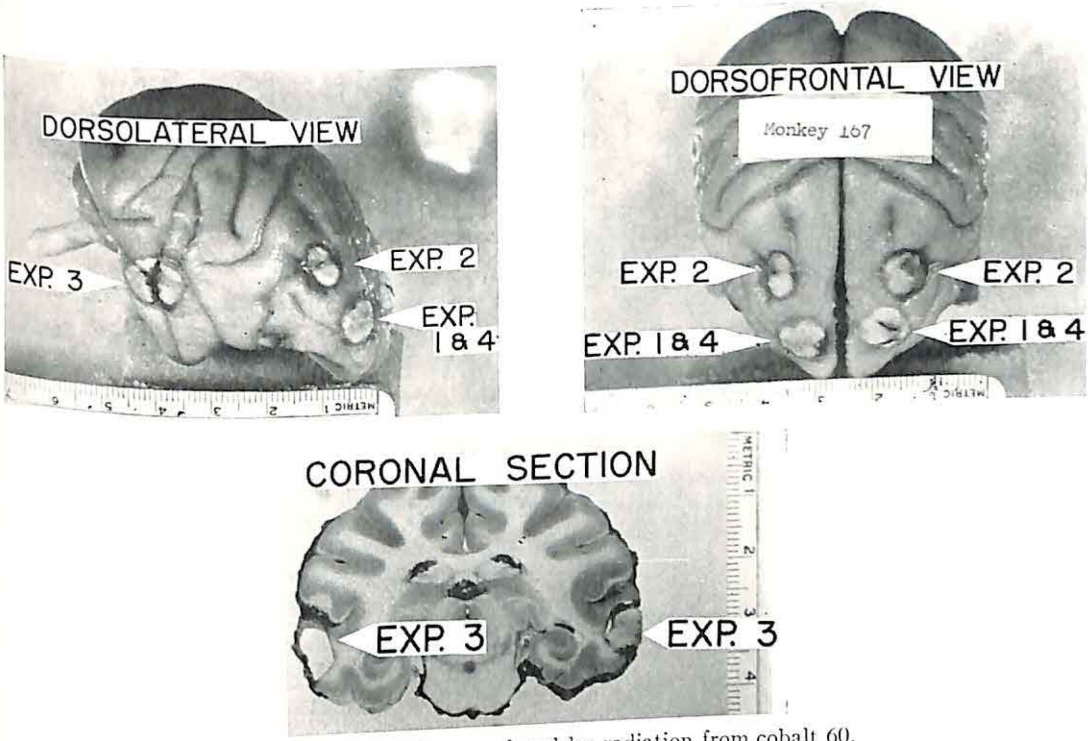

FIG. 1. Cortical lesions produced by radiation from cobalt 60.

responded effectively in the test situation, and recovery of efficient delayed-response performance began! Recovery was assumed to be complete on day 8, and during the next consecutive 20 days the monkey was given 20, 10-sec. delayed-response trials and 20 two-trial discrimination problems.

EXPERIMENT 2. EFFECT OF BILATERAL PREFRONTAL COBALT 60 IMPLANTATION ON DELAYED-RESPONSE AND TWO-TRIAL DISCRIMINATION PERFORMANCE

Method

Monkey 167 again served in this study. Information gained from experiment 1 and the subsequent 20 training days indicated that it was possible to present a two-test battery daily. Accordingly, 10-sec. delayed response was chosen as one test because of its established record as an effective indicator of prefrontal damage, and two-trial discrimination was selected as a second test. Discrimination learning has been shown to be useful as an indicator of temporal lobe involvement (3), and two-trial discrimination provides more information for daily performance assessment than other discrimination techniques. Recovery was first tested 24 hr. after implantation and is measured against the mean score on the last four preradiation test days.

Radiation dosage consisted of 8000 r. at a distance of 5 mm. from the center of each of the two needles, which were so placed that the centers of the cobalt sources were at the surface of the prefrontal cortex (see Fig. 1).

Results

The performance of monkey 167 in experiment 2 is shown in Figure 3, which indicates that recovery on both tests began about the fifth or sixth day and continued for 15 to 20 days.

Between experiments 2 and 3, *S* was given eight additional training days on 10-sec. delayed response and two-trial discrimination.

EXPERIMENT 3. EFFECT OF BILATERAL TEMPORAL COBALT 60 IMPLANTATION ON DELAYED-RESPONSE AND TWO-TRIAL DISCRIMINATION PERFORMANCE

Method

On the basis of experience gained from experiments 1 and 2 it was concluded that a dosage of 8000 r. was adequate for producing the irradiation syndrome, that a test battery which included both delayed response and two-trial discrimination was desirable, and that a formal preoperative measure should be defined. The measure selected was performance on the last 4 days of a training sequence of not less than 20 days. It was also decided to standardize the postoperative testing period at 20 days.

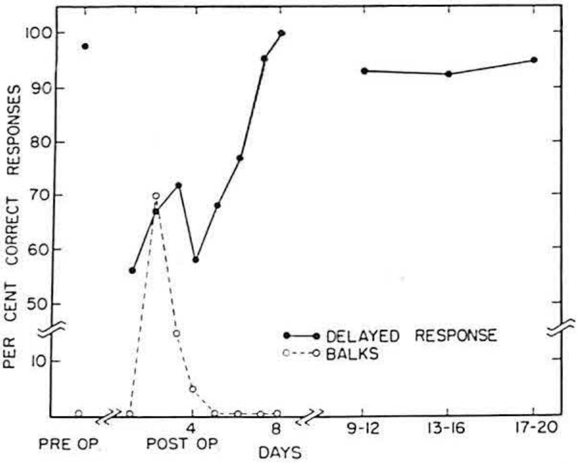

FIG. 2. Effects of irradiation of bilateral prefrontal areas by cobalt 60. Balks = refusal to respond within 60 sec. on any trial.

Results

Experiment 3 was run under these conditions, and the results presented in Figure 4 show that the course and nature of the deficit following temporal implantation were similar to those following frontal implantation of cobalt 60. The preliminary experiments gave no indication of cortical localization of radiation effects, although subsequent experiments suggest that such effects may exist.

The protocols on general behavior show that the monkey was completely unable to test on the first postoperative day. Number 167 demonstrated no startle response and no aggressive response to rough handling. It paced restlessly in the home and test cages. The monkey reached for food but consistently missed it, smelled food but did not eat it, and occasionally bumped its head while pacing around the cage. On day 2 the monkey completed all test trials even though it showed apparent convulsive behavior in the form of twitching of ears and limbs. The animal pawed at empty food wells, reached for but missed food, and brought its empty hand to its mouth. The monkey performed efficiently from day 3 onward.

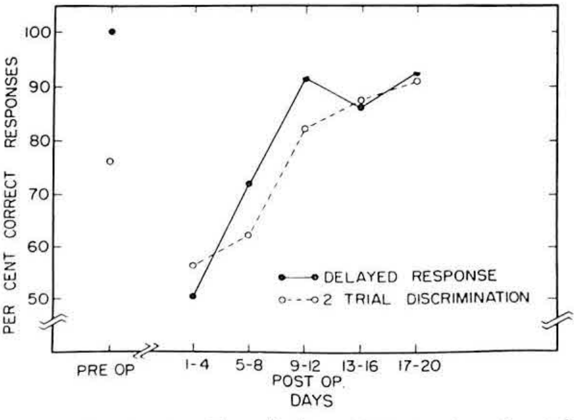

FIG. 3. Effects of irradiation of bilateral prefrontal areas by cobalt 60.

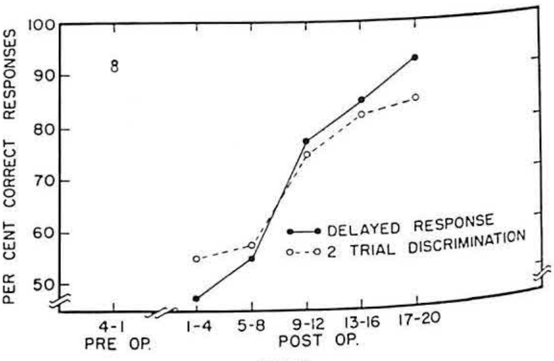

FIG. 4. Effects of irradiation of bilateral temporal areas by cobalt 60.

Because of the indications of visual disturbance, ten trials on the two crossed-strings test (4) were added to the daily test load, starting on postoperative day 3. No final conclusions can be drawn because of the lack of preradiation data, but the failure of the animal to make significant improvement on this simple test during the first 17 test days is indicative of disturbance.

Following the twentieth postoperative day, animal 167 was given eight additional days of training on 10-sec. delayed response, two-trial discrimination, and the crossed-strings test during a two-week period. On the last four training days performance on delayed response, two-trial discrimination, and the crossed-strings test was at 85, 83, and 95 per cent correct responses, respectively.

EXPERIMENT 4. EFFECT OF UNILATERAL FRONTAL COBALT 60 IMPLANTATION ON DELAYED-RESPONSE, TWO-TRIAL DISCRIMINATION, AND CROSSED-STRINGS PERFORMANCE

The data from Experiment 3 indicated that it was practical and probably advantageous to add the crossed-strings test to the battery. Having demonstrated that the cortical irradiation syndrome could be produced by bilateral temporal as well as frontal lesions, we worked to determine the effect of unilateral implantation and took a calculated risk in reducing the radiation dosage.

Radiation dosage consisted of 4000 r. calculated at 5 mm. from the tip of a needle implanted in the right prefrontal cortex. The resulting lesion was partly lateral to, and partly coextensive with, that produced by the initial implantation.

Postradiation testing was conducted for the standard 20 days, but the monkey never surpassed 70 per cent correct performance on any test and evidenced no progressive improvement on any test. Furthermore, the animal's general health and vitality showed drastic deterioration. It was assumed that these changes were delayed effects resulting from the progressive dosage accumulations of earlier radiations. Monkey 167 was maintained for 60 days after the termination of experiment 4 and tested on seven, six-trial discrimination problems 5 days a week. Trial 2 to 6 performance never exceeded 83 per cent and showed no improvement after the third day. When the animal was sacrificed at the end of this period, its weight had dropped from a high of 7.1 kg. to 4.8 kg.

The data suggested that the "cortical irradiation syndrome" could be produced by unilateral implantation, but because of the general debility of *S*, the results were far from definitive.

EXPERIMENT 5. EFFECT OF UNILATERAL COBALT 60 IMPLANTATION AND EXTIRPATION ON DELAYED-RESPONSE, TWO-TRIAL DISCRIMINATION, AND CROSSED-STRINGS PERFORMANCE

Experiment 5 was conducted with monkey 212 as *S*. This animal was given 17 days of preliminary delayed-response training and then 20 days' testing on the standardized delayed response, two-trial discrimination, and string test battery. On the last 4 days its performance in terms of correct responses was 72, 98, and 100 per cent, respectively.

Monkey 212 was then given a 4000-r. dosage calculated at 5 mm. from the radiation source on the right prefrontal cortex lateral to the superior frontal sulcus. At the end of the period of irradiation, suction was used to aspirate all tissue which was estimated to have been destroyed by the radiation energy.

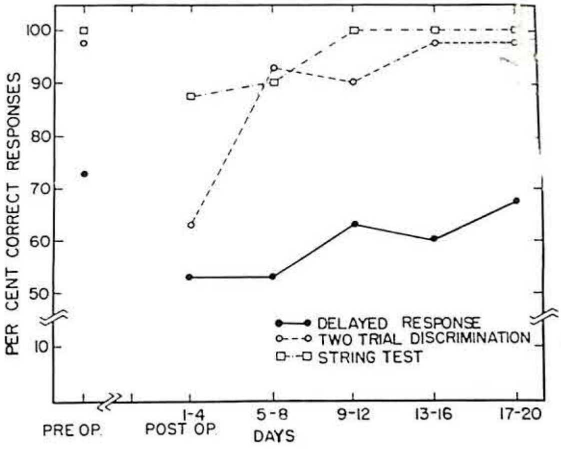

FIG. 5. Effects of irradiation of a unilateral frontal area by cobalt 60.

Results

The data presented in Fig. 5 show that unilateral implantation and subsequent extirpation produced as drastic impairment in performance on all three tests as had bilateral cobalt 60 implantation in *S* 167. It was presumed that the effects were caused by the cortical irradiation inasmuch as small, prefrontal lesions surgically produced have not been attended by loss on learned performances. Because of the individual characteristics of animal 212, it was deemed necessary, however, to have reservations about any conclusions, for its preirradiation history was one of test unreliability. Furthermore, on the delayed-response trials preceding the cobalt 60 treatment, its performance level was far lower than desirable for animals to be used in brain-damage experiments.

EXPERIMENTS 6 AND 7

Two experiments were conducted with 212 as the *S* to determine the effects of gamma radiation on the monkey's behavior when presumably no lesion was produced. The technique was to subject the animal to a 4000-r dosage delivered simultaneously by each of two needles whose tips rested on the surface of the cortex and whose radiation source was 5 mm. distant. The needles were bilaterally placed on the prefrontal cortex. Because radiation dosage from the needle source follows the inverse square law, total radiation dosage should have been less under the conditions of experiments

6 and 7 than under the conditions of the preceding experiments.

Results

Monkey 212 showed apparent loss on all three tests during the first 10 days of testing in experiment 6, and the recovery curves were similar to those previously obtained. Approximately 50 days of testing were subsequently carried out in an effort to stabilize performance on the three tests, and experiment 7 was then initiated. During the first two postimplantation days monkey 212 refused to complete the standard series on any test but performed at a level significantly beyond chance on the completed trials. The difficulty appeared to be motivational and led the *E*s to doubt that a true loss of learning capabilities existed. Performance from day 4 on was as normal as any *E* had obtained from this relatively intransigent animal.

The unavailability of any other highly trained monkeys at this time necessitated termination of the preliminary experiments.

SUMMARY AND CONCLUSION

1. Implantation of radioactive cobalt 60 with a dose of either 8000 or 4000 r. at 5 mm. from the source produces immediate total loss of previous laboratory-learned behaviors and subsequent recovery during a 20-day period.

2. This cortical irradiation syndrome can be produced by either bilateral or unilateral implantations in either the anterior or posterior association areas.

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Calvin Perry Stone

The present volume is dedicated to Calvin Perry Stone, first editor of the *Journal of Comparative and Physiological Psychology*.

His devotion to research, his enthusiasm for his profession, and the courage and integrity he demonstrated in all his endeavors set an inspiring example to all who had the privilege of working with him. As editor, author, teacher, and researcher, Dr. Stone will be remembered always as one of the great and good men who shaped the course of modern psychology and passed on to others a heritage of scientific ideals.

THE FUNCTIONAL INDEPENDENCE OF TWO DISCRIMINATION HABITS ASSOCIATED WITH A CONSTANT STIMULUS SITUATION[1]

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A basic assumption of the continuity hypothesis in discrimination learning is that all aspects of the stimulus situation impinging on the organism at or near the time of reinforcement tend to become associated with the rewarded response (6, 7). Lashley (3), Krechevsky (2), and others, however, have assumed that (*a*) the animal's behavior on any given trial is correlated with only a limited number of the impinging stimulus aspects, and that (*b*) the set of stimulus aspects correlated with the response changes at various stages of learning. They have not suggested a mechanism by means of which this could be achieved. Discrimination reversal studies usually have been interpreted as favoring the continuity hypothesis (1, 5).

Tentative support for the noncontinuity hypothesis has been suggested by a recent study employing a different experimental design from that of the discrimination reversal studies (4). Animals were trained to discriminate on the basis of one and then the other of two randomly paired stimulus dimensions. The interpretation of the results was that, once a discrimination had been established on the two cues of one stimulus dimension, it was not broken down or eliminated while the animal responded to the second stimulus dimension, even though during this latter training the animal was being randomly reinforced and nonreinforced on each of the two cues of the original discrimination. The present experiment attempts to substantiate this finding in a better controlled situation and in addition to suggest a mechanism that would make possible discrimination behavior of a noncontinuity type.

The design of the experiment is as follows. The subjects (*S*s) are trained in a discrimination situation where two stimulus dimensions, brightness and hurdles, are randomly paired on successive trials, i.e., the two combinations of cues, black high hurdles vs. white low hurdles and black low hurdles vs. white high hurdles, occur equally often and in mixed order. The *S*s first are trained to respond to one cue as positive, e.g., white. This training results in the two cues of the second dimension, high and low hurdles, being randomly reinforced and nonreinforced from trial to trial. When the *S*s reach the criterion on this brightness discrimination, the reward then is correlated with one of the hurdle cues, e.g., high hurdles. During the learning of this second discrimination, the two brightness cues, black and white, are being reinforced and nonreinforced randomly. On the third discrimination, the reward is correlated again with one of the brightness cues; on the fourth, it is correlated with one of the hurdle cues; and so on until the *S*s complete six discriminations.

According to the continuity hypothesis as outlined by Spence (6), each time the *S*s are responding to a cue on one dimension, e.g., white, the two cues on the other dimension, e.g., high and low hurdles, tend to become equal in habit strength, for each is being reinforced and nonreinforced an equal number of times. Thus, during the learning of the second discrimination the first discrimination is lost or nullified. If this is true, however, then, when the *S*s reach the third discrimination involving the same two brightness cues as the first discrimination, it should be immaterial in terms of rate of learning as to which of these two cues is made positive and which is made negative. The *S*s should learn equally rapidly whether the positive cue on this third discrimination was the positive cue on the first discrimination or whether it was the negative cue on the first discrimination.

If, on the other hand, the *S*s tend to respond selectively to the stimulus aspects in the situation, such indifference to the two cues on the third discrimination need not be expected. Rather, the expectation would be that the *S*s would show positive transfer between the first and third discriminations when the positive cue was the same in each and negative transfer between them when the positive cue of the third discrimination was the negative cue of the first. A justification for these statements is given in the discussion section.

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[1] This study was supported in part by a research grant from the Behavioral Sciences Division of the Ford Foundation.

In the design of this experiment, one additional feature is essential, however, to satisfy the requirements of the continuity hypothesis. According to this hypothesis, whether or not the difference in strength of the two cues of the first discrimination is completely nullified during the training on the second discrimination depends upon the total number of reinforcements and nonreinforcements each of these cues receives. As it is impossible to compute the required number in advance, the alternative is to have subgroups of *S*s that receive different amounts of overlearning on the second discrimination. If with this precaution there still is no evidence of a decrease in the degree of positive and negative transfer between the first and third discriminations as the amount of overlearning increases, it will be fairly strong evidence against the continuity hypothesis as now formulated.

METHOD

The *S*s were 40 pigmented rats, half males and half females, ranging in age from 100 to 150 days at the beginning of the experiment.

The discrimination apparatus has been more fully described previously (4). It consisted of a starting box leading by means of a 2 in.-wide alley into the narrow end of a V-shaped choice chamber. At the broad end of the V were the entrances to two goal boxes, each 4 in. by 4 in. by 15 in. Each box contained a food well at the far end. A sliding door at the entrances to the boxes prevented retracing. The entire apparatus was painted a mid-gray. The goal boxes were covered by a glass lid, and the rest of the apparatus with wire mesh.

The *S*s were maintained on a 22-hr. hunger rhythm. Food and water were available to them for 2 hr. following each day's training trials, after which the food was removed. After taming, the *S*s were adapted to the apparatus for ten trials by being forced to run for food in a mid-gray goal box which half the time was on the left and half the time on the right of the apparatus.

On each trial of the experiment proper one goal box was white and the other was black. The right-left order of these was varied from trial to trial. On half the trials the white box contained four equally spaced high hurdles consisting of plywood strips $1\frac{1}{4}$ in. high, and the black box contained four low hurdles $\frac{1}{4}$ in. high. On the other half of the trials the high hurdles were in the black box and the low hurdles in the white. The hurdles were always the same brightness as the goal box. The sequence of trials was so arranged that neither of the two brightness cues occurred in a given spatial position for more than two trials in succession. The same was true of the two hurdle cues. In addition neither of the two hurdle cues occurred with the same brightness cue for more than two trials in succession.

All *S*s first were trained on a brightness discrimination with black positive for half the *S*s and white positive for the other half. The food reward always was correlated with a given brightness irrespective of whether that goal box contained high or low hurdles. Five trials a day at 10-min. intervals were given until each *S* had reached a criterion of 13 correct choices out of 15 consecutive trials. A rerun method was used. If it made an error, *S* was picked up, immediately returned to the starting box, and run again until it chose correctly. Thus a trial consisted of one correct choice.

Upon completing the brightness discrimination, all *S*s then were trained on a hurdle discrimination by the same method and to the same criterion. The food reward always was correlated with a given hurdle cue irrespective of whether the goal box was white or black. High hurdles were positive for half the *S*s and low hurdles positive for the other half. All four possible combinations of positive brightness cue on the first discrimination and positive hurdle cue on the second discrimination occurred with equal frequency.

Upon reaching the criterion on the second discrimination, the 40 *S*s were divided into two major groups of 20, hereafter referred to as the Change of Dimensions (CD) and Change of Dimensions with Reversal (CDR) groups. Each of these was divided into four subgroups of 5 *S*s. In so far as possible the *S*s in these eight subgroups were equalized in terms of sex, rate of learning on the first two discriminations, and the combinations of positive cues they had experienced.

All CD *S*s upon completion of the hurdle discrimination were returned to the brightness discrimination with the positive brightness cue for each *S* the same cue as had been positive on the first discrimination. The fourth discrimination was again hurdles, with the positive cue the same as the positive cue on the second discrimination. The fifth discrimination was brightness and the sixth was hurdles. Thus the odd-numbered discriminations for a given *S* involved brightness with the same cue always positive, and the even-numbered ones involved hurdles with the same cue always positive.

All CDR *S*s upon completion of the hurdle discrimination were returned to the brightness discrimination but with the positive brightness cue for each *S* on this discrimination the same as the negative cue on the first discrimination. The fourth discrimination was again hurdles but with the positive cue the same as the negative cue on the second discrimination. The fifth discrimination was again brightness, and the sixth was hurdles. Thus the odd-numbered discriminations for a given *S* involved brightness, but each time *S* returned to this dimension the positive and negative cues were the reverse of *S*'s previous experience with them. Similarly, the even-numbered discriminations involved hurdles, but each time *S* returned to this dimension the positive and negative cues were the reverse of *S*'s previous experience with them.

The four subgroups in the CD and CDR groups differed in the amount of overlearning they were given on each discrimination except the first before starting the next. All *S*s reached the criterion on the first discrimination and immediately began the second. Upon reaching the criterion on the second discrimination, however, 5 *S*s in each major group were given zero

TABLE 1

Illustrative Training Schedule Showing Positive Cue

Group	Overlearning Trials	Discrimination 1	2	3	4	5	6
CD	0 20 40 100	B	H	B	H	B	H
CDR	0 20 40 100	B	H	W	L	B	H

trials overlearning, i.e., they proceeded immediately to the next discrimination, 5 were given 20 trials overlearning, i.e., they continued for 20 trials beyond the criterion before going to the next discrimination, 5 were given 40 trials overlearning, and 5 were given 100 trials overlearning. The *S*s in each subgroup received this same amount of overlearning on the third, fourth, and fifth discriminations. The over-all design of the experiment is illustrated in Table 1.

Because of the amount of time involved in running the 100 trials overlearning subgroups, these *S*s were run only on the first four discriminations rather than all six. In addition, on the third discrimination, but not on the second, the overlearning trials for these *S*s were given at the rate of 10 per day. Thus, while the data from these groups are comparable to those of the other subgroups during the learning of the third discrimination, they are not strictly comparable on the fourth. One *S* in each of the 100 trials overlearning subgroups died during the experiment.

RESULTS

The equality of matching between the eight subgroups is shown graphically in Figure 1. An analysis of variance of these data for discriminations 1 and 2 is shown in Table 2. This indicates that the subgroups tended to learn at comparable rates during this period when they were all treated exactly alike. The only component reaching significance is the mean difference between the two discriminations, presumably due to the fact that (*a*) the hurdle discrimination was a somewhat harder problem than the brightness discrimination (4), and that (*b*) the shift to the hurdles was prolonged because of the previous training on the brightness discrimination.

The third discrimination provides the first test of the difference between the CD and CDR groups. At this point both groups returned to the brightness discrimination, but for the CD group the positive cue was the same as the positive cue on the first discrimination, whereas for the CDR group the positive cue was the negative cue of the first discrimination. The analysis of variance based on scores to the criterion for this third discrimination also is shown in Table 2. The two main findings are: (*a*) the CDR group on the average takes significantly more trials (.01 level) to master this discrimination than does the CD group, and

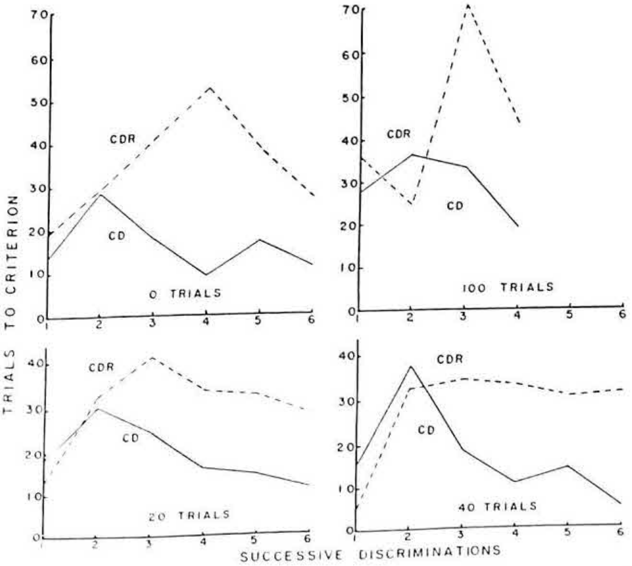

FIG. 1. Each of the above figures represents the CD-CDR contrast on successive discriminations for a given amount of overlearning. Each point is based on five *S*s except for the 100 trials overlearning group; here only four *S*s are represented.

TABLE 2
Results of Analysis of Variance

Component	Discriminations 1 & 2		Discrimination 3		Discriminations† 4, 5 & 6	
	df	Var.	*df*	Var.	*df*	Var.
1. Discriminations	1	3369.3*		—	2	429.2
2. CD vs. CDR	1	88.8	1	4168.5*	1	10,780.3*
3. Overlearning	3	284.4	3	1221.8**	2	245.9
a. 0, 20, 40		—	2	76.5		—
b. 100 vs. 0, 20, 40		—	1	3512.6*		—
4. Interactions						
a. 1 × 2	1	167.0		—	2	173.6
b. 1 × 3	3	492.5		—	4	63.9
c. 2 × 3	3	99.6	3	282.0	2	147.5
d. 1 × 2 × 3	3	170.2		—	4	171.1
e. Animals × Discr.	30	368.0		—	48	204.3
5. Animals within subgroups	30	149.2	30	382.6	24	95.4

* .01 level of significance.
** .05 level of significance.
† Only the 0, 20, and 40 trials overlearning groups are included.

(*b*) there is no evidence of any interaction between the amount of overlearning and the CD-CDR contrast. This latter finding supports the contention that the initial brightness discrimination was not nullified even with prolonged training on the hurdles discrimination.

The other major finding in these data is the significant difference (.05 level) between the overlearning subgroups in terms of the mean number of trials required to reach the criterion on the third discrimination. When the sum of squares for this component is subdivided, there is no evidence of significant differences between the 0, 20, and 40 trials overlearning groups. Rather, the major portion of the total sum of squares is attributable to the difference between the 100 trials overlearning group and the average of the other three.

An analysis of variance of trials to criterion for the 0, 20 and 40 trials overlearning groups on discriminations 4, 5, and 6 is shown in Table 2. The only component reaching significance (.01 level) is the difference between the CD and CDR groups. There is no evidence that the amount of overlearning had any significant effect on the rate of learning these discriminations, nor is there any evidence of an interaction between the amount of overlearning and the CD-CDR contrast.

Because on the third discrimination the 100 trials overlearning group was given its overlearning trials at the rate of 10 per day, the data of this group were handled separately for the fourth discrimination. An analysis of variance of these data indicates that the difference between the CD and CDR means is in the same direction and as large as for the other three overlearning groups on this discrimination, but with so few degrees of freedom it falls between the .05 and .10 levels of significance.

DISCUSSION

From the point of view of a continuity theory, there are two possible ways of interpreting these results. The first assumes that hurdle and brightness differences act as two independent stimulus dimensions, i.e., there is no "afferent neural interaction." On this assumption, the continuity hypothesis predicts that the difficulty of learning the third discrimination increases with increasing amounts of overlearning on the second discrimination. The overlearning strengthens the hurdle discrimination and makes it harder to extinguish when brightness is again the relevant dimension. The results for the third discrimination support this conclusion in part, although there is no simple relationship between overlearning and trials to criterion. As indicated previously, the significant difference between overlearning subgroups is due almost entirely to the 100 trials overlearning group. Nor is there any consistent evidence of such a relationship for discriminations 4, 5, and 6, as can be seen in Table 2. On this assumption about independent stimulus dimensions, the continuity hypothesis also predicts that with increasing overlearning on the second discrimination the difference between the CD and CDR groups on the third discrimination should progressively decrease. The overlearning on the hurdles not only tends to fixate this discrimination, but at the same time it tends to nullify any residual discrimination on the brightness cues. Thus, while the absolute difficulty of the third discrimination should increase for both the CD and CDR groups, the difference in difficulty for these two groups should decrease with overlearning. The data for the third discrimination and succeeding ones fail to show any evidence of such an interaction factor.

The alternative assumption available to a continuity hypothesis is that the stimulus dimensions are not independent. Instead, the stimulus situation must be conceptualized as though containing just four cues: (*a*) black-high, (*b*) black-low, (*c*) white-high, and (*d*) white-low. The implications of this for the training of the CD and CDR groups is illustrated in Table 3. It is apparent that on the third discrimination the CD group must reverse the black-low and white-high cues whereas the black-high and white-low cues retain the same positive and negative values as in the previous two discriminations. The CDR group, on the other hand, must reverse the black-high and the white-low cues whereas the black-low and the white-high remain unchanged. Thus, each time the CDR group goes to a new discrimination, it must reverse a pair of cues that have been building up differential habit strength during the previous two discriminations. The CD group, however, need reverse a pair of cues that has had only one preceding discrimination on which to establish differential habit strengths. The result is that the CDR group would find it harder to learn the new discrimination than would the CD group because of the differential amounts of training of the cues to be reversed.

The design of the experiment does not rule out this interpretation completely, but the present results are against it. This interpretation implies that the CDR group is poorer than the CD group on the third discrimination because it must reverse a pair of cues that have had an average of 35 trials additional training, i.e., the 20 trials on the first discrimination plus the 15 criterion trials. If the 0, 20, and 40 trials overlearning subgroups within the CD and within the CDR groups are considered, however, it is apparent from the analyses in Table 2 that overlearning a discrimination to this extent has little if any effect on the rapidity with which the third and subsequent discriminations are mastered. The only evidence in the experiment that overlearning has any effect on the rate of mastery of a new discrimination comes from the 100 trials subgroups on the third discrimination, and even this effect tends to disappear on the fourth discrimination.

TABLE 3

Illustrative Analysis of Training Schedule

Group	Stimulus	Discrimination and Positive Cue			
CD	Pairs	1 B+	2 H+	3 B+	4 H+
	a	BH+ WL−	BH+ WL−	BH+ WL−	BH+ WL−
	b	BL+ WH−	BL− WH+	BL+ WH−	BL− WH+
CDR		1 B+	2 H+	3 W+	4 L+
	a	BH+ WL−	BH+ WL−	BH− WL+	BH− WL+
	b	BL+ WH−	BL− WH+	BL− WH+	BL+ WH−

On the noncontinuity assumption, a mechanism can be suggested that would account for the present results. The proposed mechanism perhaps can be made clear in terms of an illustration. Assume that the stimulus situation is arranged so that the black-white cues always are placed at the top of the apparatus and the two hurdle cues at the bottom. Then in order to learn the first discrimination, where white is positive, the *S*s must learn two things: (*a*) they must learn to orient toward the top of the apparatus, and (*b*) they must learn to prefer the white over the black. To master the second discrimination, where high hurdles are consistently but brightness cues only randomly rewarded, the *S*s must extinguish the original orientation habit, learn its converse of looking down, and establish a preference for high over low hurdles. Further, assume that during the first few trials on the second discrimination, while the *S*s continue to respond with their original habits, the orientation habit of looking up extinguishes more rapidly than does the preference for white over black. This implies that the *S*s begin orienting downward and responding systematically to the high hurdles even though the discrimination on the brightness cues remains.

If, now, the reward again is correlated with one of the brightness cues, the *S*s once more must learn to orient upward. Once this habit is reinstated, however, they will show considerable positive transfer between the first and third discriminations if white is again the positive cue. Their original preference for white over black has remained despite the interpolated training on hurdles. On the other hand, they will show negative transfer between the first and third discriminations if black is now the positive cue, for then they must reverse their preferences on the brightness dimension.

This formulation postulates two learning processes occurring simultaneously, the development of orientation behavior and the establishment of stimulus preferences. It permits selective responding because the orientation behavior determines which set of cues impinges on the organism at any one time. At the same time, the assumption that these two classes of behavior are learned and extinguished at differential rates allows the preference for one stimulus aspect to retain its habit strength and remain nonfunctional even though it is present in the physical environment while the *S*s are systematically reacting to other stimulus aspects.

This illustrated mechanism appears inappropriate for the present experiment because of the lack of any spatial separation between the sets of stimuli used. But even if it is assumed that the sensory input contains all four stimulus aspects on a given trial, it is conceivable that two analogous learning processes are involved. One, corresponding to the overt orientation behavior, would involve the identification of and reaction to a dimension or set of stimuli, and the second would involve the establishment of preferences between stimuli within a set. If, then, it is assumed that the first of these processes is established and extinguished more rapidly than the other, it is apparent that the *S*s would be responding systematically to one stimulus set without modifying their preferences for the other set, even though the latter was impinging on their sense receptors during this time. This implication seems to be the core contention of the noncontinuity hypothesis and fits in well with the results of the present experiment.

It is apparent that this roughly sketched mechanism is designed to account for some of the phenomena usually ascribed to "set" and "attention" (cf. 4, 8). It has no bearing on the controversy between "expectancy" and "S-R" formulations. Either one can allow for it if it proves to have any merit. Rather, its main implication is that there can be hierarchical dependencies between habits such that many types of transfer and related phenomena cannot be predicted on the basis of the continuity assumption as presently formulated.

SUMMARY

Forty pigmented rats were divided into eight subgroups of five each. All groups were trained in a discrimination situation involving two stimulus dimensions, high-low hurdles and black-white, which were paired randomly on successive trials. The sequence of discriminations learned by four of the subgroups, the Change of Dimensions (CD) groups, was as follows: (*a*) brightness with black positive, (*b*) hurdles with high positive, (*c*) brightness with black positive, (*d*) hurdles with high positive, (*e*) brightness with black positive, and (*f*) hurdles with high positive. The other four subgroups, the Change of Dimensions with Reversal (CDR) groups, learned the same first two discriminations, but on the third white was positive, on the fourth low was positive, on the fifth black was positive, and on the sixth high was positive. Starting with the second discrimination, one subgroup from each of the CD and CDR groups had zero trials overlearning, one 20 trials, one 40 trials, and one 100 trials. The 100 trials overlearning groups did not complete the fifth and sixth discriminations.

1. The CD groups on the average mastered the third through the sixth discriminations significantly more rapidly than did the CDR groups.

2. Only on the third discrimination was there any evidence that the amount of overlearning increased the difficulty of the succeeding discrimination.

3. There was no evidence on any of the discriminations of an interaction between the amount of overlearning and the CD-CDR contrast.

4. These results were interpreted as opposed to the continuity hypothesis. A noncontinuity mechanism was described that would account for them.

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SOME PROPERTIES OF THE WARNING STIMULUS IN AVOIDANCE BEHAVIOR

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Previous experiments have demonstrated the feasibility of establishing and maintaining avoidance behavior without the use of an exteroceptive warning signal (11, 12). The stable rates of responding generated by this procedure, and the reproducible distributions of inter-response times (13), provide sensitive base lines from which to measure the effects of other variables in the avoidance situation. The present investigation describes changes in the characteristics of avoidance behavior that result from the introduction of a stimulus prior to each impending shock.

METHOD

Subjects

Four cats, 2 males and 2 females, and 12 male white rats comprised the total number of subjects (*S*s) employed.

Apparatus

The lever-pressing apparatus for the rats, with its associated automatic control and recording devices, has been described previously (12, 13). The only addition was a small neon pilot light with a white hood located 5 in. above the lever and inaccessible to the rats because of a clear plastic false ceiling interposed between it and the lever. This light, flashing once per second, was the warning stimulus preceding shock.

The experimental box used for the cats was a 2-ft. cube. An electrifiable grid composed the floor and one side, while the other three sides were made of galvanized iron. A plate glass top was also used as a sliding door for insertion and removal of the animals. The lever, a 2-in. square of aluminum, was located 2.5 in. above the grid floor during original training, but was raised to a height of 10 in. prior to the present experimentation. The shock intensity, held constant throughout for a given cat, was set at values just high enough to maintain consistent levels of behavior. These values ranged from 2 to 4 ma. for the several cats.

Procedure

Nondiscriminated avoidance. The basic procedure has been reported previously (11). In summary, a brief shock (S_2) occurred at regular intervals, e.g., 20 sec., unless the lever was pressed. Every time the animal emitted the avoidance response, the shock was postponed an additional 20 sec. The animal received a shock each time 20 sec. elapsed without a lever press. The time by which each response delayed the shock will be termed the *R-S*$_2$ interval. Holding the lever down following a press did not prevent the shock from occurring.

Discriminated avoidance. The same contingencies were in effect, but with the addition of a stimulus before a shock was due. For example, if the animal permitted 15 sec. to elapse without a lever press, a warning stimulus (S_1) appeared and remained until terminated by a response or a shock, whichever occurred first. Each response in the absence of S_1 postponed *both* S_1 and S_2. Thus both stimulus and shock were subject to control by the animal. The time by which each response delayed the warning stimulus will be termed the *R-S*$_1$ interval, while the time between stimulus onset and shock, if no response occurred, will be termed the S_1-S_2 interval.

The shock duration was fixed at 0.2 to 0.3 sec. for both rats and cats. The warning stimulus was a light for the rats and a clearly audible tone for the cats. The rats ran on alternate days, 6 to 7.5 hr. per day, while the cats ran in daily 2-hr. sessions.

RESULTS

Changes in response rate following introduction of the warning signal are illustrated in Figure 1. When compared to prior base levels established over five consecutive sessions (35 hr. for the rats and 10 hr. for the cats) without the signal, the response rates show a marked decline as a result of the change in procedure. The decline, however, does not necessarily occur as early or as precipitously as is shown in Figure 1.

Figure 2 provides information on the relation between the rate measure and a more conventional indicator of the establishment of a conditioned avoidance response. The *R-S*$_1$ interval for this animal was 15 sec., and the *R-S*$_2$ interval was 20 sec. That is, if the animal waited 15 sec. without responding, the signal appeared, and if it waited 20 sec., it received a shock. The measure, "per cent of stimuli discriminated," gives the probability of an avoidance response in the presence of the signal. It is obtained by dividing the number of responses during the signal by the total number of signals and multiplying by 100. It may be noted that the rate decline is accompanied by an increase in the percentage of stimuli discriminated. Session 1 provides a control for the expected probability of responses at comparable points in time when the stimulus was not employed. The significance of sessions 11 and 12 will be discussed below. This measure is analogous to the "per cent conditioned responses" indicator generally used in avoidance experiments, the one difference being that in the present situation the onset of the stimulus is under the control of the animal. (Although several investigators have used procedures in which "extra" responses were permitted to delay the occurrence of a "trial," none has reported quantitative data on the frequency of such controlling responses [5, 6, 10].)

Along with the decline in rate produced by the warning stimulus, a striking change appears in the temporal distribution of avoidance responses. This change is reflected not only in the responses that occur during the S_1-S_2 interval, but also in those emitted prior to the onset of S_1. A typical example is presented in Figure 3, in which cumulative distributions of the time intervals between successive responses are plotted for two sessions. The S_1 (tone) appeared whenever the animal waited 20 sec. without responding, and was terminated by a shock 10 sec. later if the avoidance response did not intervene. By session 27 a relatively stable state had been reached in which approximately 60 to 65 per cent of the avoidance responses occurred in the presence of the stimulus. Only 25 to 30 per cent of the responses were emitted in the absence of the stimulus. The difference may be accentuated by omitting from consideration the large proportion of responses separated by intervals of 2 sec. or less. These rapid bursts of responses, reported previously (13), are typical and unexplained.

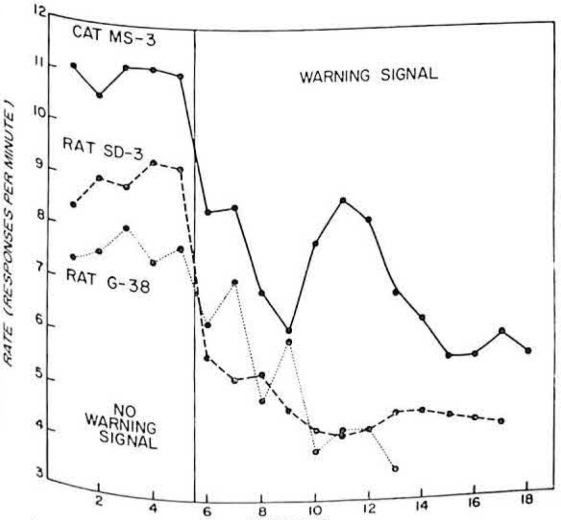

FIG. 1. Effect of the warning signal upon the response rate. The R-S_1 interval was 15 sec. and the R-S_2 interval was 20 sec.

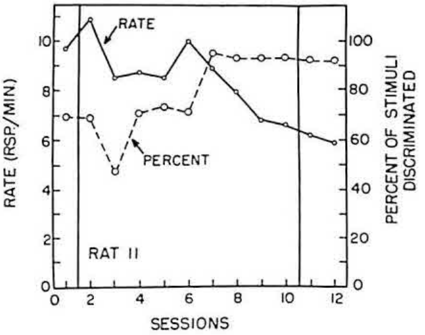

FIG. 2. Effect of the warning signal upon response rate and percentage of stimuli discriminated. Warning signal present only during sessions 2 to 10.

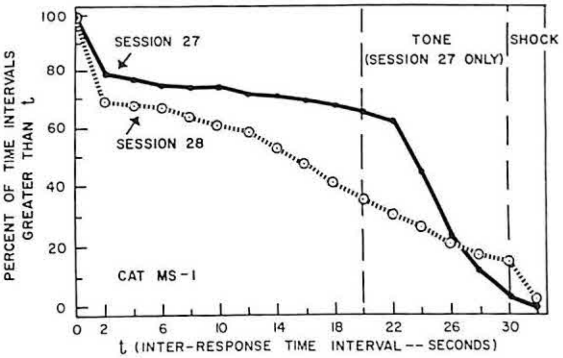

FIG. 3. Cumulative distribution (per cent) of inter-response times with and without the warning signal.

The distribution of responses in time was quite different when the warning signal was omitted in the following session. That portion of the distribution preceding the 20-sec. interval displayed a steeper slope, while no discontinuity was apparent between 20 and 30 sec. The majority of responses were separated by 20 sec. or less, as contrasted to the preceding session in which the majority of inter-response intervals fell between 20 and 30 sec.

When the warning signal was omitted, after extended discrimination training, the distribution of inter-response times for all cats assumed the same form as that shown in the curve for session 28, Figure 3. The relatively low proportion of short inter-response times has been interpreted previously (13) as a temporal discrimination. In the case of the cats, however, the precision of this time dis-

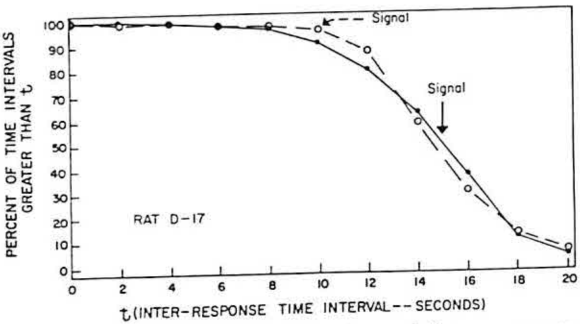

FIG. 6. Cumulative distributions of inter-response times after a temporal discrimination has been strongly established. The stimulus was introduced at 15 sec. (solid curve) and at 10 sec. (broken curve).

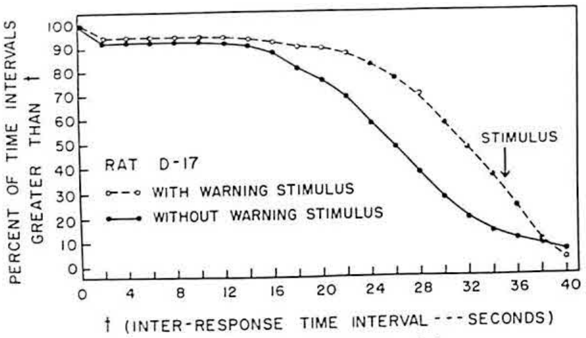

FIG. 7. Cumulative distributions of inter-response times after establishment of a temporal discrimination. $R\text{-}S_2 = 40$ sec. The dashed curve illustrates the change resulting from introduction of the warning signal at 35 sec.

appeared during 28 hr. of training without the stimulus, and the final distribution is shown for session 32.

These data are sufficient to demonstrate two points: (*a*) the stimulus and time discriminations are separate phenomena, as indicated by their differential rates of acquisition, and (*b*) in its early stages, the formation of the time discrimination is linked with the presence of the warning stimulus. This is indicated by the absence of the temporal discrimination during the 91 hr. prior to introduction of the stimulus (sessions 1 to 13), by its failure to maintain itself initially in the absence of the stimulus (sessions 15 and 16), and its lack of improvement after the stimulus was withdrawn (sessions 29 to 32) in spite of its rapid development in the immediately preceding hours (sessions 23 to 28).

The degree of control exercised by the time discrimination was checked in several ways with one animal. First, the stimulus procedure was reinstated with an $R\text{-}S_1$ interval of 15 sec. This produced no change in the inter-response time distribution. When the $R\text{-}S_1$ interval was changed to 18 sec., again no difference was observable. The $R\text{-}S_1$ interval was then changed to 10 sec., with the results illustrated in Figure 6. The difference between the curves, approximating the maximum intersession variability for this animal, are so slight as to demonstrate further the resistance of the time discrimination to control by the stimulus that generated it. After this determination, the stimulus was again removed and the $R\text{-}S_2$ interval changed from 20 to 40 sec. The new distribution, after 35 more hours of training, appears in the solid curve of Figure 7. With the longer $R\text{-}S_2$ interval, the animal's timing was much more variable, as shown by the more gradual slope of the curve from 16 to 40 sec. When the stimulus was then imposed upon this less precise temporal discrimination, its effect was much more pronounced (Fig. 7, broken curve). However, the stimulus effect was still not powerful enough to produce the sharp control observed in the cats (Fig. 3) or in the earlier stages of the stimulus procedure with the rats (Fig. 5, session 28).

DISCUSSION

The Stimulus Discrimination

Mowrer and Lamoreaux (8) suggest that avoidance responses appear in the absence of S_1 because of generalization of fear from "situation with S_1" to "situation without S_1." The eventual decline of such "extra" or "spontaneous" responses (7, 8) is held to occur because they do not accomplish any fear reduction, i.e., they produce no change in "situation without S_1."

The present experiments, demonstrating the effects of the signal against a base line of nondiscriminated avoidance behavior, suggest a different approach to the discriminative process. The existence of nondiscriminated avoidance responses prior to introduction of a warning signal indicates that responses in the absence of S_1 possess an independent source of reinforcement. It is not sufficient simply to consider them a nonreinforced product of stimulus generalization.

Identification of this reinforcement, in a specific experimental situation, was first suggested by Hefferline (2); was later confirmed in detail by Winnick (16); and was generalized to all avoidance situations by Schoenfeld (9). The latter's formulation points out that nonavoidance behavior may become aversive through a Pavlovian process of close pairings with shock; that the avoidance response is never closely paired with shock and is, therefore, the least aversive of all the organism's behavior; and finally, that the avoidance response is reinforced in an operant fashion (14) by terminating an aversive sample of nonavoidance behavior.

According to this formulation, an avoidance response in the absence of S_1 does change the situation, in that other ongoing behavior is terminated and replaced by a less aversive condition. With respect to the decline of avoidance responding in the absence of S_1, the relevant question becomes, "Why is the termination of nonavoidance behavior no longer reinforcing?"

The answer may be found in the Pavlovian discrimination that follows upon introduction of the warning stimulus. Nonavoidance behavior is paired with shock only in the presence of S_1, never in its absence. When not in compound with S_1, such behavior loses its aversive properties, and its termination no longer reinforces the avoidance response.

In addition to the decreased probability of response in the absence of S_1, there occurs an increased probability in the presence of the signal. It has been suggested that the signal provides a more discriminable aversive situation (1) and that its termination adds an extra amount of reinforcement for the avoidance response (9). Strong evidence for this interpretation is provided by experiments demonstrating more rapid acquisition of a discriminated avoidance response when the latter terminates S_1 than in a trace-conditioning procedure (7, 8). Such an explanation, however, raises an additional problem. If S_1 provides an additional aversive element in the situation, it may be asked why the frequent occurrence of the warning signal is not sufficient to maintain the aversive properties of nonavoidance behavior. That it does not do so to any great extent is indicated by the low probability of the avoidance response in the absence of S_1.

Additional evidence of the relation between the present data and that obtained by means of other avoidance conditioning procedures comes from a study by Kamin (3), who investigated the effects of the S_1-S_2 interval with a trace-conditioning procedure. He found a slower acquisition rate during the S_1-S_2 interval as a function of increasing S_1-S_2 intervals. At long intervals, then, the response effective in postponing the shock was not under the discriminative control of S_1, and the procedure became very similar to the nondiscriminated avoidance technique used here. The increasing rate of "spontaneous" responses as a function of increasing S_1-S_2 intervals, as observed by Kamin, is thus consistent with the analysis proposed above.

The Time Discrimination

Animals trained with the nondiscriminated avoidance procedure typically form a poorly developed time discrimination (13). Since nonavoidance behavior emitted just after a response or a shock never produces an immediate shock, behavior occurring at such times becomes less aversive. Avoidance responses and shocks initiate "safe periods," during which the probability of an avoidance response is relatively low. The present data raise the problem of how the warning signal functions to increase the duration and persistence of the safe period to the point where it maintains itself even after the signal is no longer presented.

Two observations lower the validity of any explanation based only on the data at hand. The first of these is the superior performance by the rats, as compared with the cats, with respect to the temporal discrimination, a difference opposite that expected on the basis of the evolutionary level of the two species. The second is the resistance to stimulus manipulation displayed by the well-established temporal discrimination in the rats. One possible effect of the warning signal is, however, worth noting.

When the stimulus discrimination is well formed, the majority of avoidance responses are accompanied by termination of the signal. Presumably the combination of the two events provides a more discriminable and longer lasting stimulus ("trace") during the safe period than does the response alone. In the case of a light-sensitive animal such as the white rat (4), it is possible that the aftereffect of even a dim flashing light is greater than that of other stimuli. Once a prolonged safe period has been set up on the basis of such stimulus aftereffects, whatever "clock" mechanism the animal simultaneously develops, be it behavioral (15) or physiological, has an opportunity to take over the discrimination alone when the warning signal is removed. With this formulation, several lines of future inquiry are evident.

SUMMARY

Using white rats and cats as *Ss*, avoidance behavior was conditioned with a procedure that does not involve an exteroceptive warning stimulus. The rate and temporal distribution of the nondiscriminated avoidance responses were used as base lines from which to observe changes resulting from the introduction of an exteroceptive warning signal prior to each shock.

In the discrimination procedure, the probability of occurrence of the avoidance response increases in the presence of the warning signal and decreases in its absence. In addition, in the case of the rats at least, the discriminated avoidance procedure facilitates development of a temporal discrimination. This discrimination eventually acquires a degree of control over the behavior which, under some conditions, may actually surpass that exercised by the stimulus.

The changes in rate and temporal distribution observed in discriminated avoidance behavior were discussed in terms of a Pavlovian discrimination. Nonavoidance behavior in the absence of the signal loses its aversive properties and is able to compete successfully with the avoidance response except when the signal is present.

Facilitation of the time discrimination by the warning signal was tentatively attributed to discriminable temporal properties of the stimulus.

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THE EFFECT OF A RACHITOGENIC DIET ON THE HOARDING BEHAVIOR OF RATS[1]

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In a former study (1) the hoarding behavior of rats was measured before and after they had been placed on a vitamin-B deficient diet for 40 days. During each test the animals were presented with both normal and vitamin-B deficient pellets. After the deprivation period the rats hoarded significantly greater percentages of the normal pellets than they had before the deprivation period. It was also demonstrated that after the animals had been returned to a normal diet and retested, they hoarded about the same percentages of normal and vitamin-B deficient pellets as they had during the predeprivation tests and significantly smaller percentages of normal pellets than they had on the postdeprivation tests.

It was the purpose of the present experiment to study the hoarding behavior of rats before and after they had been placed on a rachitogenic diet. The plan of the experiment was similar to that of the former study.

METHOD

Subjects

Twenty-five male and female Wistar albino rats and eight male and female hooded rats were used. The animals were between 32 and 45 days old when placed on the rachitogenic diet.

Apparatus

The apparatus used in these experiments is essentially the same as that used in the former study (1). It consists of nine screen-covered alleys, each having a living cage at one end and a food bin at the other. The food bin is divided into two equal parts by a partition. Each compartment contains one type of pellet used in the experiment. The end of the food bin is closed off to prevent escape of the animal.

All pellets (actually small discs) were made with the same apparatus used in the former experiment and were approximately the same size (¾ in. in diameter and ⅛ in. thick). The average weight of the normal pellets was 2.0 gm. and that of the rachitogenic pellets, 1.9 gm.

Normal pellets were made by mixing ground Purina Dog Chow Checkers with milk-sugar and water. The rachitogenic pellets were made with similar proportions of diet, milk-sugar, and water. The rachitogenic diet, mixed according to USP specifications, consisted of 76 per cent ground whole yellow corn, 20 per cent ground gluten, 3 per cent calcium carbonate, and 1 per cent sodium chloride.

Procedure

All animals were fed exclusively on Purina Rabbit Chow or Purina Dog Chow Checkers from the time they were weaned until they were used in the experiment. Before the predeficiency tests, the animals were placed in the apparatus from two to seven days to permit them to adjust to the new situation and to explore the alley. During this period they were provided with an excess of Rabbit Chow or Chow Checkers in their living cage during the late afternoon and night, but the food was removed for about 7 hr. during the day. This practice of removing all food for about 7 hr. during the day was continued in all hoarding tests.

Before the animals were placed on the deficient diet they were tested daily for six to seven days. During each test period the animals were permitted to hoard both types of pellets for 30 min., after which the food bins were removed. The animals were permitted to eat from the pellets they hoarded for about 20 min., after which the hoarded pellets were removed from the living cage and Rabbit Chow or Chow Checkers provided, as indicated above. Throughout the hoarding tests, the positions of the normal and deficient pellets were changed in the food bins according to a chance sequence to avoid the influence of position habit on the choice of the pellets hoarded.

Animals were placed on the deficient diet for prescribed periods of time and then given daily postdeficiency tests for six to seven days. Additional tests were run on animals returned to the normal diet after they had been on the deficient diet.

Statistical Treatment of the Data

The statistical techniques used in the present study are identical with those reported in the former study (1, 3). The percentage of normal pellets hoarded was determined for each hoarding-test period. These percentages were then transformed to *thetas*, and the significance of the difference of dichotomous proportions (normal vs. deficient) pellets was determined for the following: (*a*) the difference between the percentages of normal pellets hoarded during the predeficiency period and during the postdeficiency tests; (*b*) the difference between the percentages of normal pellets hoarded during the predeficiency tests and the tests following the return to the normal diet; and (*c*) the difference between the percentages of normal pellets hoarded during the postdeficiency tests and the tests following the

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[1] These experiments were made possible through a grant-in-aid from the Institute of Research, Lehigh University.

return to the normal diet. A p beyond the .001 level is regarded as significant.

RESULTS

Experiment I

Four animals (litter A) were weaned on Rabbit Chow and tested. The animals were then fed the deficient diet for 20 days and retested. No *S* hoarded significantly greater percentages of normal pellets than it had on the predeficiency tests (animals no. 1 to 4, Table 1). Animal no. 4 hoarded significantly more deficient pellets during the postdeficiency tests.

Experiment II

Four animals (litter B) were weaned on Rabbit Chow and tested. The animals were then fed the deficient diet for 31 days and retested. Animals no. 5 and 6 (Table 1) hoarded significantly greater percentages of normal pellets than in the control period. Animal no. 7 hoarded significantly more deficient pellets, and animal no. 8 showed no change in its hoarding behavior.

Experiment III

Twelve animals (litters C, D, and E) were weaned on Rabbit Chow and tested. The animals were then fed the deficient diet for 40 days and retested. Eleven of the 12 rats hoarded significantly greater percentages of normal pellets than during the predeficiency tests (animals no. 9 to 14 and 16 to 20, Table 1). Examination of the daily records of the remaining animal (no. 15) revealed that from the third to the seventh hoarding tests it chose normal pellets 100 per cent of the time. On these five hoarding tests the animal showed the same preference as the other 11 animals.

After the postdeficiency tests the animals were given a special mixed-pellet test for which the partition was removed from the food bin and both kinds of pellets intermingled. Eight

TABLE 1

Results obtained from Experiments I–III

Ltr = litter; *An* = animal; *Tst* = hoarding tests; *Pre* = predeficiency hoarding; *D* = number of days on B-diet; *RN* = hoarding after return to normal diet; *NL* = number of normal pellets hoarded; *TL* = total number of pellets hoarded; % = per cent normal pellets hoarded.

Experiment I					
Ltr	An	Tst	NL	TL	%
A	1	Pre	103	212	49
		20D	137	268	51
	2	Pre	161	299	54
		20D	214	413	52
	3	Pre	148	224	66
		20D	223	375	59
	4	Pre	191	309	62
		20D	168	341	49
Experiment II					
B	5	Pre	160	317	50
		31D	176	246	72
	6	Pre	115	192	60
		31D	125	157	80
	7	Pre	167	258	65
		31D	179	355	50
	8	Pre	151	300	50
		31D	262	472	56

Experiment III					
Ltr	An	Tst	NL	TL	%
C	9	Pre	116	235	49
		40D	221	240	92
		RN	175	281	62
	10	Pre	105	158	66
		40D	87	88	99
		RN	171	176	97
	11	Pre	109	244	45
		40D	178	178	100
		RN	277	396	70
D	12	Pre	87	156	56
		40D	193	277	70
		RN	142	184	77
	13	Pre	56	165	35
		40D	260	293	89
		RN	188	304	62
	14	Pre	28	59	47
		40D	197	208	95
		RN	165	199	83

Experiment III					
Ltr	An	Tst	NL	TL	%
E	15	Pre	113	210	54
		40D	115	199	58
		RN	274	450	61
	16	Pre	26	100	26
		40D	250	279	90
		RN	153	241	63
	17	Pre	30	110	27
		40D	226	251	90
		RN	154	216	71
	18	Pre	115	299	38
		40D	365	401	91
		RN	342	378	90
	19	Pre	31	209	15
		40D	113	124	91
		RN	140	340	41
	20	Pre	157	272	58
		40D	310	314	99
		RN	240	279	86

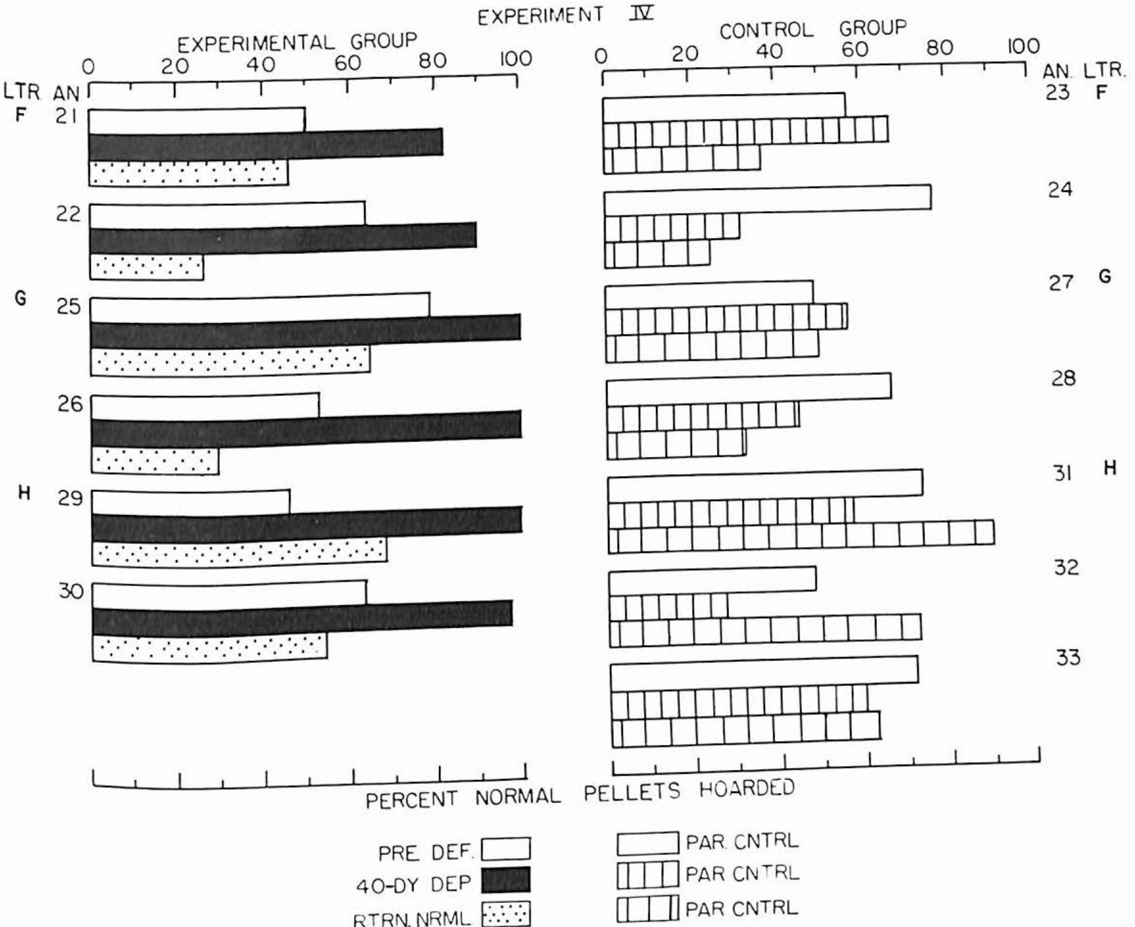

FIG. 1. Per cent normal pellets hoarded for the experimental and control animals of experiment IV. *An* = animal; *Ltr.* = litter; *Pre def.* = hoarding tests before the animals were placed on the deficient diet; *Par. cntrl* = parallel control; *40-Dy. Dep.* = hoarding tests after being fed the rachitogenic diet; *Rtrn. nrml*—hoarding tests after the animals had been returned to the normal diet. Hoarding scores are included in Table 1.

of the ten animals which had hoarded 90 per cent or more normal pellets at the end of the deprivation period, hoarded 79 per cent or more normal pellets during these tests. The preference tended to be preserved.

After the mixed-pellet tests the animals were returned to the normal diet for periods of 56 to 86 days. During this period the animals were occasionally given free access to small dishes of cod-liver oil. Eight of the 12 animals now hoarded significantly smaller percentages of normal pellets than during the postdeficiency tests (animals no. 9, 11, 13, 14, 16, 17, 19, and 20). The remaining four animals continued to hoard about the same percentages of normal pellets as they had during the postdeficiency tests. Ten of the 12 animals, however, hoarded greater percentages of normal pellets than they had during the predeficiency tests (animals no. 10 to 14 and 16 to 20), and the remaining 2 animals hoarded about the same percentages of normal pellets as during the predeficiency tests (no. 9 and 15).

Experiment IV

Thirteen animals (litters F, G, and H) were weaned on Purina Dog Chow Checkers instead of the Rabbit Chow. Each litter was divided into an experimental and control group. After the predeficiency tests, the animals in the experimental group were fed the rachitogenic diet for 40 days, while the animals in the control group continued on the Chow Checker diet. The data obtained from the 13 animals are presented in Figure 1.

All six animals in the experimental group hoarded significantly greater percentages of normal pellets at the end of the deficiency period than they had during the predeficiency tests (animals no. 21, 22, 25, 26, 29, and 30). On the other hand, the animals in the control group hoarded approximately the same percentages of normal pellets as they had during the first hoarding tests (animals no. 23, 27, 28, 31, 32, and 33). There was no significant change in their behavior. Animal no. 24 hoarded a significantly smaller percentage of normal pellets than it had during the first hoarding tests.

After the postdeficiency tests the animals of the experimental group were fed Chow Checkers supplemented with cod-liver oil for 120 days and then retested. All six animals now hoarded significantly smaller percentages of normal pellets than during the postdeficiency tests (no. 21, 22, 25, 26, 29, and 30). Of the seven control animals, three showed no significant change in their hoarding behavior (no. 24, 27, and 33). Two hoarded significantly greater percentages of normal pellets than they had during the postdeficiency tests (no. 31 and 32). Two animals hoarded significantly smaller percentages of normal pellets than they had during the postdeficiency tests (no. 23 and 28).

When the percentages of normal pellets hoarded at the end of the predeficiency tests were compared with those of the tests 120 days or more after the first predeficiency test, the following results were obtained: Four of the six experimental animals now hoarded about the same percentages of normal pellets as they had during the predeficiency tests (no. 21, 25, 29, and 30). Two animals hoarded significantly smaller percentages than they had during the predeficiency tests (no. 22 and 26). Five animals of the control group hoarded about the same percentages of normal pellets as they had during the predeficiency tests (no. 23, 27, and 31, 32, and 33). Animals no. 24 and 28 hoarded significantly smaller percentages of normal pellets than they had during the predeficiency tests. No animal in either the experimental or control groups hoarded significantly greater percentages of normal pellets at the end of the experiment as compared with the predeficiency tests.

Deficiency Symptoms

Comparison of the members of the experimental and control animals of experiment IV at the end of the 40-day deprivation period showed the following differences. The weight of the experimental group was about 55 per cent of that of the control group. The animals were undersized and their fur shaggy. Most animals showed weakness in their hind legs. These symptoms were also typical of the animals in experiment III which were also fed the deficient diet for 40 days.

After the rachitogenic animals were fed the normal diet, supplemented with cod-liver oil, their weight increased and the physical symptoms tended to disappear. The weight of the experimental animals of experiment IV now rose to 86 per cent of the weight of the control animals.

DISCUSSION

Under the present experimental conditions it has been demonstrated that 16 of 17 animals placed on a rachitogenic diet for 40 days hoarded significantly greater percentages of normal pellets than on the predeficiency tests, while the animals in the control groups showed no significant change in their hoarding behavior. Only 2 of 4 animals fed the deficient diet for 31 days and not one of 4 animals fed the deficient diet for 20 days showed a significant change in their hoarding behavior. Feeding the animals a normal diet supplemented with cod-liver oil tended to reverse the hoarding behavior. No general statement can be made regarding the comparison of the percentages of normal pellets hoarded after the animals were returned to the normal diet and the percentages of normal pellets hoarded during the predeficiency tests, since there was no consistent trend in the data.

Other investigators studying the same problem have used short periods of deprivation with results similar to those obtained in the present experiment for the 20 and 31 days of deprivation. Wilder (4) tested young rats in a maze situation before and after placing them on a rachitogenic diet for 9 to 35 days and found no significant change in their behavior. Harris *et al.* (2) mention that they studied the question using the free-selection technique but also obtained negative results. Finally, Young and Wittenborn (5) used the preference technique and failed to find a change in behavior after 21 days of deprivation. None of the investigators cited above used periods of deprivation of 40 days, thus preventing further comparisons with the present experiment. The length of the deprivation period appears to be critical.

The results obtained in the experiment are in agreement with those obtained in the vitamin-B deficiency study (1). Animals which had been deprived of vitamin B for 40 days hoarded significantly greater percentages of normal pellets at the end of the deprivation period than during the predeficiency tests. Feeding the animals a normal diet supplemented with the deficient vitamin changed the hoarding behavior, making it similar to that of the predeficiency tests. The animals now hoarded about the same, or lower, percentages of normal pellets, as during the predeficiency tests.

SUMMARY

Young hooded and white rats of both sexes were tested in a hoarding situation before and after being fed a rachitogenic diet for various lengths of time. Short periods of deprivation (20 days) produced no preference for normal pellets in 4 animals. Longer period of deprivation (31 days) produced a preference for normal pellets in 2 out of 4 animals; however, deprivation for longer periods of time (40 days) produced preference for normal pellets in 17 out of 18 animals. The preference was retained when the position of the normal pellets was changed, and when the two types of pellets were mixed in a common bin. Feeding the animals a normal diet after the deprivation period resulted in a reduction of the percentages of normal pellets hoarded as compared with those hoarded during the postdeficiency tests.

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EFFECTS OF HYPOPHYSECTOMY ON BEHAVIOR IN RATS: III. THERMOREGULATORY BEHAVIOR[1]

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Thermal homeostasis in a warm-blooded animal, such as the rat, is achieved through effective regulation of heat production, absorption, and conservation (2). To a large extent, production is controlled by hormones of the thyroid and the adrenal cortex, both of which are under hormonal influence from the anterior lobe of the hypophysis. Thus, loss of the hypophysis is followed by some loss in the animal's ability to adjust to the lower ranges of temperatures encountered in the laboratory or its native habitat (5, 6, 7, 8, 10).

If the drop in environmental temperature is neither large nor precipitous, a hypophysectomized rat may preserve its life and maintain a fair degree of vigor by effective utilization of compensation mechanisms within its repertoire (10). For example, huddling or lying beside warm objects facilitates heat absorption; horripilation and "balling up" so as to cover hairless regions of the body reduces radiation; and nest construction from insulating materials, when available, effectively conserves the heat of one individual or several rats encapsulated by the nest.

In the present experiments two types of compensatory adjustment by hypophysectomized rats were investigated: (*a*) nesting at various temperatures within the ranges ordinarily found in a colony room, and (*b*) preferential responses to contrasting temperatures in a runway that permits complete freedom of movement between relatively warm and relatively cool locations.

NEST CONSTRUCTION BY MALE RATS

Method

Two experiments on nesting by albino rats will be reported. In the first, 18 hypophysectomized and 19 like age controls of the Sprague-Dawley strain were used. Operations[2] were performed when they were 35 days old, and the 10-day test period embraced the age span of 51 to 60 days. On day 1 the operates averaged 89 gm. and the controls, 167 gm., in weight. Very little change occurred in the mean of the hypophysectomites, but that of the controls increased at the usual rate for this strain of rats.

During nesting tests all animals were individually housed in wire mesh cages with metal floors (dimensions, in inches, 24 by 18 by 12). Thirty-two of these cages were enclosed in plywood boxes, 55 by 31 by 31 in., four to the box and so spaced that air circulated freely within them. The plywood boxes formed a circle about a heater by means of which the upper ranges of temperatures could be maintained as demanded by the thermal schedule. Each plywood box is provided with a small blower that directs room air into the chamber; at the rear are small holes that provide a ventilating outlet. Five cages were not enclosed by these boxes. These served as a check on the possible influence of the plywood boxes. Around the entire setup was placed a heavy canvas tent which tended to dim the daylight and to equalize air currents and diurnal variations in heat for all the *Ss*. To obtain the lower ranges of temperature, windows of the building were opened at night, thereby causing temperature within the tent gradually to assume the outdoor temperatures of 58° to 65° F. No provision for precipitous lowering of temperatures during day- or nighttime was available in this laboratory.

The cages were supplied daily with water, Morton's salt cake, and a fresh supply of food consisting of the following: ground horse meat, McCollum mixture (finely ground wheat, oats, and yellow corn; powdered whole milk, casein, $CaCo_3$, and NaCl), orange, lettuce, and carrot. The nesting materials consisted of a ½-in. layer of wood shavings spread evenly over the metal floor and covered by approximately 60 gm. of crisp shredded newspaper. This amount of paper, when properly arranged in a corner of the cage and supported by shavings, enabled the rat to encapsulate itself completely, as many of them actually did.

Cages for operates and controls were so distributed inside the tent that like conditions were shared by both groups. During the day (8 A.M. to 8 P.M.) the tent temperatures varied from about 75° in the morning to 90° at midafternoon. The night temperatures on the ten test nights were made to approximate the following varying schedule: 60°, 60°, 88°, 88°, 76°, 80°, 66°, 64°, 84°, and 64° F. Each evening at approximately 4 P.M. the cages were inspected. If any nesting had taken place during the day, the shavings and paper were distributed evenly over the floor of the cage to insure that all animals started from a common base. On the following morning, at 8 A.M., the nests were independently rated by three investigators previously trained in using an adaptation of the Stone-Walker (11) rating scale given in Table 1. Room temperature was then brought quickly

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[1] Financial support for this investigation was provided by the National Science Foundation (NSF—G 343).

[2] Hypophysectomy performed by the Hormone Assay Laboratories, Chicago, Ill.

TABLE 1

Scale for Rating Nests Built by White Rats (Modification of Scale Used by Stone & Walker [11])

Rating	Characteristics
0—No nest	No movement of paper and shavings
1—Trace of nest	Less than ¼ of paper moved to form ring or low platform
2—Poor nest	Nest is not compact, uncovered, and less than ½ of paper used
2.5—	Same as 2 except ½ or slightly more of the paper used
3—Fair nest	Nest is compact, uncovered, and most of the paper is used
3.5—	Amount of paper used, somewhere between a 2 and a 3, but the nest is covered
4—Good nest	Nest is covered, and compact, not scattered; most of the paper used
4.5—	Same as 4 except some of the shavings are used
5—Excellent nest	Nest is covered, all paper used, and all the shavings swept up around the base

within the daytime range by cooling or by supplemental heat. Also, nests were completely destroyed soon after the ratings were completed.

For the second series of tests 25 males of the Sprague-Dawley strain were used. Of these 12 were hypophysectomized at the age of 35 days, and the others were controls. Their mean weights were slightly higher than those of the first group. The chronological age of the operates and 6 of the controls was 78 days at the beginning of the nesting tests; the remaining controls were 91 days of age. These animals were housed in a light- and soundproof room equipped with refrigerating and heating units. Metal cages identical with those described above were used for housing and were so distributed that small differences in temperature in different corners of the room were shared alike by both groups. From 8 A.M. to 4 P.M. the room temperature was maintained within the range of 75° to 80° F. At 4 P.M., the refrigeration unit was activated, thereby dropping the room temperature quickly to the level of 50° to 60° F., where it remained throughout the night. Lights were off from 5 P.M. to 8 A.M., but on during the rest of the day. At 8 o'clock each morning three investigators rated the nests independently, as in the preceding experiment.

This study ran for only four consecutive days, for in that time it was apparent that the more elaborate controls of environmental stimuli (light, sound, relatively constant temperatures) did not yield results that differed essentially from those obtained in the first experiment.

Results from First Nesting Study

Figure 1 graphically presents the means of the three daily ratings for the ten-day period. The fact that many good nests were built on the first night is noteworthy, since none of these animals had ever been isolated with nesting materials prior to this time. Although a rating of 5 was possible, provided the rat used all the paper to encapsulate itself and also moved the shavings up around the base of the nest, none of the rats in this study ever obtained that rating. Only rarely, in our experience, do males move both the shavings and paper as is done by parturient females (11). Comparatively speaking, the hypophysectomites tended to build bigger nests and to encapsulate themselves more frequently than the controls when temperatures were below the normal, daytime ranges, and both groups refrained from elaborate nest construction when room temperature was very high. These results support the supposition that nest construction and utilization are heat conservative behavior and that when heat production is lessened, as in the hypophysectomized rats, a greater amount of nest utilization is evoked (4, 5, 6, 7, 8, 10). Fewer operates sat upon a nest mound, where a large amount of the body is exposed, than was the case with the controls. Figure 2 shows a typical nest (rated 4.5) made by a hypophysectomite when the night temperature dropped to 60° F. Beside it is shown the floor of this rat's cage one day later when night temperature was held at 88°. At the rear of the cage (most distant from the heater), the animal had swept the shavings from the metal floor; in this poorly insulated locale it spent much of its time. In the latter case the behavior was conducive to heat dissemination rather

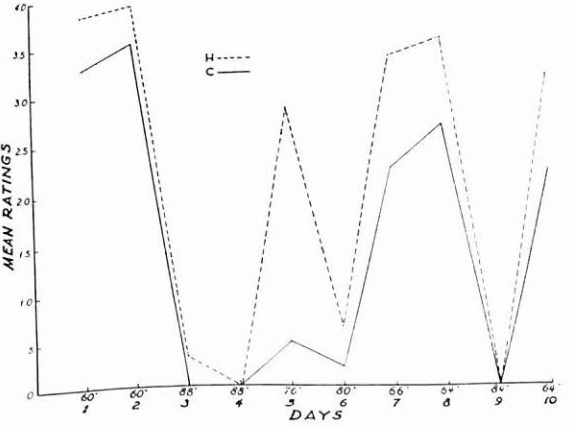

FIG. 1. Mean ratings of nests on 10 consecutive days.

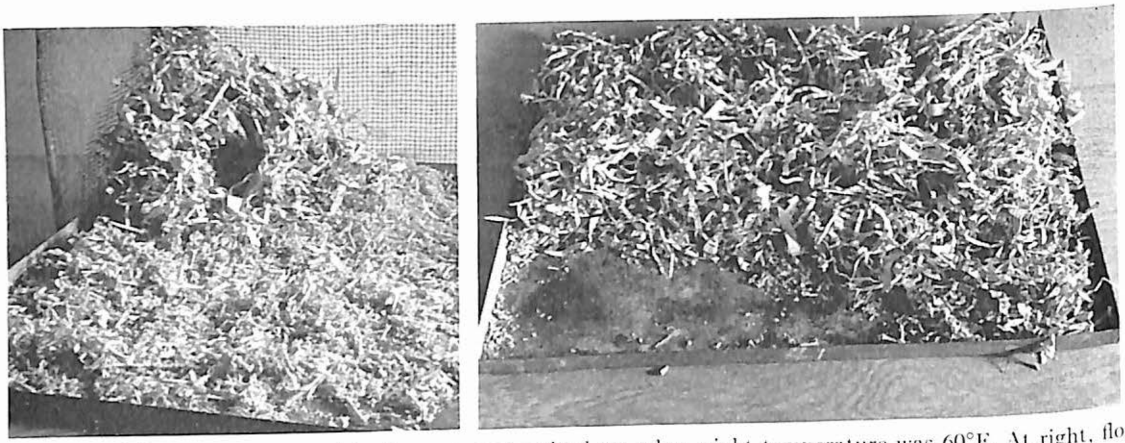

FIG. 2. At left, nest constructed by hypophysectomized rat when night temperature was 60°F. At right, floor of same cage on following day, after night temperature of 88° F. (Rating for left, 4½; for right, 0)

TABLE 2

Significance of Differences between Means of Nest Ratings

(All Differences Favor Hypophysectomites)

Day	1	2	3	4	5	6	7	8	9	10
Temp.	60°	60°	88°	88°	76°	80°	66°	64°	84°	64°
Diff.	0.56	0.40	0.32	0.00	2.36	0.42	1.14	0.88	0.01	0.95
p	$<.01$	$<.01$	$>.1$		$<.001$	$>.1$	$<.001$	$<.01$	$>.1$	$<.01$

than retention. Several rats obtained a similar result by perching upon the food bin, which was made of hardware cloth.

Table 2 indicates which differences between mean ratings of operates and controls are significant. It is evident from the results as a whole that the hypophysectomized rats clearly surpassed the controls in nest construction except when temperatures were well above the normal, daytime range. Noteworthy, however, are a few exceptions to this general tendency. Two controls consistently equaled the better nesters among the operates. No operate, however, was quite as indifferent to the use of paper as were the least active controls.

Results from the Second Experiment

The mean rating of nests by the hypophysectomites for the four-day period was 3.61 and that for the controls, 2.89. A t test yielded a significant difference between these ratings ($p = .001$). There was no progressive change in ratings from the first to the fourth day, although fluctuations for individuals on successive days were found.

On the whole, results from the first and the second experiment are harmonious in respect to the characteristic differences between hypophysectomized and normal rats. The second experiment provided some additional support for the tacit assumption that the thermal factor, as opposed to an auditory or visual factor, is primarily responsible for the instigation of nesting in our setup. Here the room was dark and soundproof during the time nests were constructed.

Autopsy records revealed small particles[3] of the hypophysis in four of the first group and four of the second group. No difference in nest construction or utilization between these hypopituitary animals and the clean-cut operates was seen.

CHOICE OF A WARM VS. A COLD LOCALE

Method

Here the problem pertains to choices of a warm as opposed to a cold locale in a narrow runway where freedom of choice was permitted. At the front of Figure 3 is shown the arrange-

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[3] We are indebted to Dr. Hadley Kirkman, Director of the Anatomy Department, and to his technician, Miss Marilyn E. Robbins, for inspecting the heads of the hypophysectomites and sectioning suspicious-looking remnants found at the site of the sella.

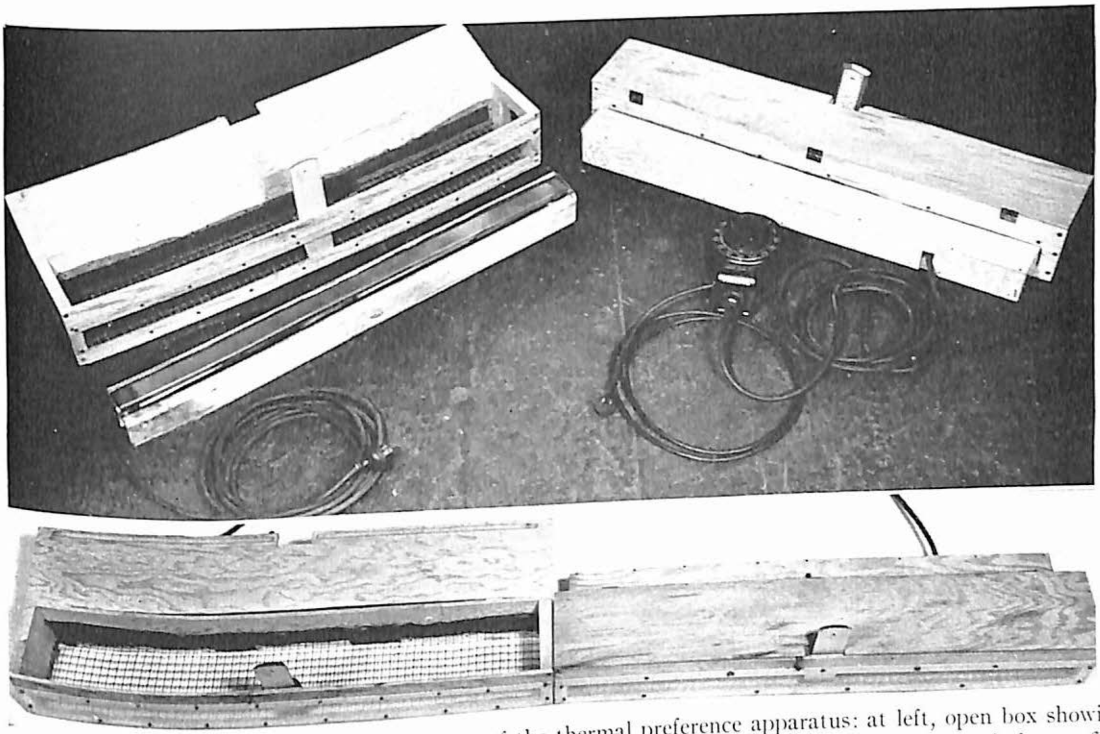

FIG. 3. At the rear are shown the main parts of the thermal preference apparatus: at left, open box showing hardware cloth floor, Plexiglas window at front, and thermometer with bulb facing opening where strip heater fits; also, strip heater, encased by wood that was lined with sheet aluminum, except on face of heater; at right, rear view of box with a strip heater fitted into place; Variac used to regulate current. Photograph at front illustrates the two boxes as they appeared to *E* while in use.

ment of two narrow alleys placed end-to-end on a table so that the opening from one to the other is continuous. At the back, disassembled pieces of the apparatus are shown. Each alley is fitted with an electric strip heater. Variacs provide a means of varying the current entering the heaters, thereby controlling heat production as required by a day-to-day schedule of thermal values presented in the two alleys. The temperature within the alleys could be read from thermometers standing directly opposite the heaters and midway in the alleys. Plexiglas windows enabled *E*, seated behind a screen, to follow the movements of the rat.

The room in which the study was conducted is well insulated and also was equipped with a refrigeration unit by means of which temperatures could be dropped to 40° F., or any intermediate value between that and the normal room temperature. The alley designated as the cold box for the day was allowed to assume the temperature of the refrigerated room. The warm box was held at normal room temperature or heated to any desired value up to 100° F. Thus, the rat could choose between coming to rest in a warm alley that approximated or exceeded the temperature to which it had previously been accustomed and a relatively low temperature in the range of 45° to 60° F., which we assumed would be too cold for comfort.

Preliminary trials. The 25 males used in the second nesting study were the *Ss* of the thermal preference tests. At the first preliminary test, the 12 hypophysectomites and 6 controls were 46 days old, the other 7 controls, 60 days old. The corresponding ages at the first of the main preference tests were 66 and 80 days, respectively. To accustom them to the apparatus, two series of preliminary runs were made. In the first, the animals were given 20 trials at the rate of 2 per day. They were taken from a warm room (c. 75° F.) in groups of 3 or 4 and placed at one end of the apparatus, after which they could run about ad libitum during the 2-min. period; then they were returned to an adjacent warm room. After all rats had a first turn, the second round was begun, and finally they were returned to the colony room to await further tests on the following day. The starting box was varied each day. Frequent readings of the thermometers and appropriate adjustments of the Variac enabled *E* to maintain the contrasting temperatures at the values indicated in the upper half of Table 3. For the second series of preliminary tests each exploratory period was 5 instead of 2 min. long. In general, procedures were like those described for the first runs, but the temperature of the warm box was always maintained at 75° F., while temperatures of the cold box were varied from day to day between 45° and 60°, as shown in the lower half of Table 3.

Procedures for tests proper. Prior to beginning the experiment proper the rats were divided into four subgroups for convenience of handling. Groups 1–H and 2–H each contained six randomly selected hypophysectomized animals. Similarly, the controls were divided to form subgroups 3–C and 4–C. The testing schedule was so arranged that neither group began first on two consecutive days, and daily testing followed an alternating pattern, i.e., *x-y-x-y*, where *x* and *y* represent subgroups of the H and C groups. This method was adopted in order that variables connected with the time of day at which testing occurred would be counterbalanced for groups. The schedule for the final test series is given in Table 4.

TABLE 3

Schedule for Preliminary Trials

Day	Trial	Starting Side	Temp. in Left	Temp. in Right
(First series: 2-min. exploratory period)				
1	1, 2	L.L	50°	70–75°
2	3, 4	L.L	70–75°	50°
3	5, 6	R.R	70–75°	88–95°
4	7, 8	L.L	88–95°	70–75°
5	9, 10	L.L	68–70°	80–84°
6	11, 12	R.R	80–84°	68–70°
7	13, 14	R.R	45°	70–75°
8	15, 16	L.L	70–75°	45°
9	17, 18	R.R	70–75°	88–95°
10	19, 20	R.R	70–75°	45°
(Second series: 5-min. exploratory period)				
1	1, 2	L.L	45°	75°
2	3, 4	R.R	75°	50°
3	5, 6	L.L	55°	75°
4	7, 8	R.R	75°	45°
5	9, 10	R.R	75°	55°
6	11, 12	L.L	50°	75°
7	13, 14	L.L	75°	75°
8	15, 16	R.R	75°	60°
9	17, 18	R.R	75°	75°
10	19, 20	L.L	60°	75°

TABLE 4

Schedule for Individual Trials

Day	Trial	Starting Side	Temp. in Left	Temp. in Right	Order of Running Subgroups
1	1, 2	R.L	45°	75°	1, 3, 2, 4
2	3, 4	L.R	75°	50°	3, 1, 4, 2
3	5, 6	R.L	55°	75°	2 4, 1, 3
4	7, 8	R.L	75°	45°	4, 2, 3, 1
5	9, 10	R.L	75°	55°	3, 1, 4, 2
6	11, 12	L.R	50°	75°	1, 3, 2, 4
7	13, 14	R.L	75°	75°	4, 2, 3, 1
8	15, 16	L.R	75°	60°	2, 4, 1, 3
9	17, 18	L.R	75°	75°	1, 3, 2, 4
10	19, 20	L.R	60°	75°	3, 1, 4, 2

On each test one *S* was placed in the starting box in the manner described above for groups of three. The lid was closed, temperatures were recorded, and the timer was started. Thereafter, *S*'s position within the boxes was recorded every 30 sec. (or six times) during the 3-min. observation period. The "score" for the test consists of the number of times, in the six observations, *S* was in the warm box. At the end of the test period, temperatures were again recorded and *S* was removed and returned to its cage outside the room (temp. 70° to 75° F.) to await the second trial of the day or return to the colony room.

An interval of about 25 min. separated trials 1 and 2. On trial 2, *S* was placed in the box opposite from that in which it started trial 1; otherwise the procedures were the same. Except for a period of about 1 hr. or less each day, while undergoing the thermal preference tests, all *S*s remained in the colony (at 70° to 85° F.).

Results

Results from the thermal preference tests are shown in Figure 4. Each point on the graph represents the average score for two trials (one day) of testing. Scores above "3" on the ordinate indicate that the group as a whole was checked more times in the warm box than in the cold box except for days 7 and 9. On these days, as indicated on the abscissa, temperatures of both boxes were the same. Arbitrarily, for days 7 and 9, number of times checked, at the appropriate times, in the right-hand box were plotted.

Clearly, there is a consistent tendency for

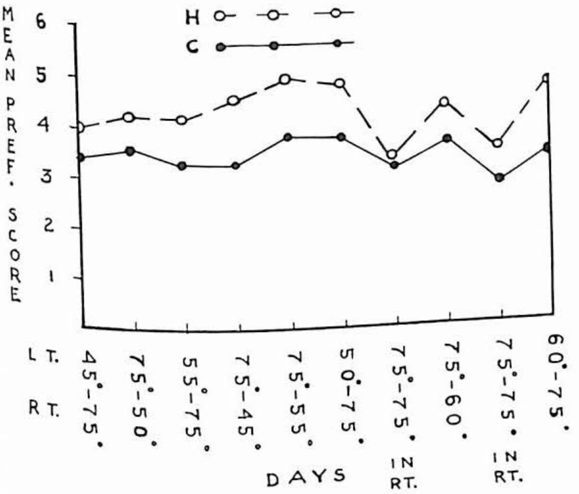

FIG. 4. Means of thermal preference scores for 10 consecutive days.

TABLE 5

Variance Table for Data from Thermal Preference Tests

Source	Sum of Squares	*df*	Variance	*F*	*p*
Between groups	19.07	1	19.07	8.55	.01
Between subjects	49.18	22	2.33		

both groups to be checked more times in the warm than in the cold box on most of the days. However, the frequency is higher for the hypophysectomites than the controls throughout the test series. The analysis of the data, summarized in Table 5, indicates that the difference between groups is statistically significant ($p<.01$). The results reported above support the conclusion that hypophysectomized rats show a stronger preference for warm environmental temperatures (greater aversion to cold?) than do normal controls.

DISCUSSION

As yet there are no data on the optimal temperature for hypophysectomized rats as determined by the von Herter method (3) of ascertaining where they come to rest along a thermal gradient. Also lacking is information on thermal needs as related to the age of *S*s, the age when operated, and the elapsed time between operation and beginning of tests. While each of these problems is important and should be investigated, the lack of evidence on them here does not vitiate our findings on nesting and preferential responses for the setups herein used. Also, having used no females at all, our interpretations are not encumbered by the special factors of estrus or maternal behavior (4, 11). However, certain other factors need to be reviewed in order that one may assess the likelihood of their giving rise to the behavioral differences herein ascribed to thermal stimuli.

Was odor consistently associated with the temperature differential in the preference setup? Although precautions were taken to minimize wood odor from the heated box by lining all points of contact between it and the heater with sheet aluminum, it is possible that heating did produce a distinctive wood odor and that by choosing the odorous box *S* would have obtained thereby a higher warm-box score. Granting such a cue, there is no a priori ground for assuming a differential preference between groups unless by consistent association with warmth in the test situation it became a secondary cue that facilitated location of the warm box. We are inclined to minimize the importance of odor as either a primary or a secondary cue because the air in the runways was constantly agitated by input-outflow action of the air conditioning apparatus. The latter would also minimize any possible influence of relative humidity as a differential factor between the two boxes. As far as known neither of the foregoing factors could have operated differentially in the nesting situations.

Did the factor of inactivity favor the hypophysectomized rats in either the nesting situation or the preference box? The answer is unequivocally negative for nesting. Our operates constructed nests more promptly than the controls at night. Also, they did more nesting during the day, when room temperatures were in the neighborhood of 75° F. and, as already indicated, made more elaborate nests at night. Conceivably, however, if the operates had been torpid or sedentary they might have maneuvered themselves into the warm box, remained there for the duration of the test period, and thus, by virtue of making few exploratory excursions into the cool box, have acquired a higher score than the more active "gad-about" controls. Not foreseeing this possibility, we failed to take notice of each excursion from one to the other box; hence, only impressions can be reported. Everyone connected with the experiment received the impression that the hypophysectomites were no less active in the preference boxes than the controls and that they exhibited a normal exploratory tendency. They appeared to be alert, curious, quick in movements, and sufficiently vigorous to move freely throughout the enclosures. No behavior suggestive of torpidity or sedentary tendency was noticed. Hence, it seems unlikely that differential activity played a decisive role in the operates' achieving the higher warm-box scores.

All things considered, it would seem that superior nesting and greater preference for the warm locale denote the presence of a higher "thermotactical optimum," in the sense of von Herter (3), in rats following loss of the hypophysis. One characteristic in the human syndrome of hypopituitarism (9) is "increased sensitivity to cold." Further investigations should be undertaken to reveal what specific factors are responsible for it. Hypophysectomy in young rats may interrupt the decline in this optimum that normally takes place between infancy and maturity. Also to be appraised are such factors as loss of subcutaneous fat, thinning of the integument, altered growth of the fur, reduction of blood supply to the skin, and lower metabolic rate. Finally, not to be overlooked is the possibility of heightened sensitivity of thermal receptors of the integument. The likelihood of such a change might profitably be explored by use of the recently developed apparatus for testing thermal discrimination described by Downer and Zubek (1).

SUMMARY AND CONCLUSIONS

1. Eighteen male albino rats, hypophysectomized when 35 days of age, were compared with 19 like-age controls in nest building on 10 consecutive nights when from 51 to 60 days old. Room temperatures were varied between 60° and 88° F. At the highest temperatures little or no nesting occurred in either group, but at all temperatures below normal, colony-room values, the operates built and utilized significantly better nests, from the standpoint of insulating devices, than the controls. Also, for 12 hypophysectomites operated at the age of 35 days, a similar degree of superiority was found, in comparison with 13 controls, when tested in a light- and soundproof room wherein nighttime temperatures were held steady with the range of 50° to 60° F. It is assumed that superior nesting is indirectly instigated by deficiency in heat production resulting chiefly from loss of the thyro- and adrenotropic hormones.

2. Two of the foregoing groups (12 hypophysectomites and 13 controls) were compared as to preferential responses for a warm vs. cold locale in a runway wherein temperature of the warm compartment was maintained at 75° F. and that of the cold box was varied from day to day over the range of 45° to 60° F. The hypophysectomized rats used the warm box significantly more than the controls. Choice of a locale affording supplemental heat is regarded as compensatory behavior in hypophysectomized rats whose mechanism for heat production has been impaired. If this interpretation is correct, the results on nesting and thermotactic preference are in harmony. More effective use of insulating materials reduces radiation, and coming to rest in the warmer room facilitates heat absorption.

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PATTERN PERCEPTION FOLLOWING INSERTION OF MICA PLATES INTO VISUAL CORTEX[1]

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Electrical field concepts of cerebral integration have not found support in earlier experimental tests in which functional organization has been observed to be but little disturbed by extensive radial slicing of the cortex or by short-circuiting of the cortical currents with implanted pins and wires of gold, tantalum, and stainless steel (2, 3, 4). However, it has not been unanimously agreed that either knife cuts or metallic inserts produce sufficient distortion of direct current flow in the cortex to make the findings definitive in so far as the electric field hypothesis is concerned. It seemed that a more effective test could be obtained by inserting into the cortex numerous plates of a dielectric material. With the cortical currents forced to detour around a series of dielectric barriers, gross distortion of their normal patterning would be inevitable. This latter approach was employed in the present study. Small plates of mica were implanted into the visual and surrounding cortex in cats, and the functional effects were tested subsequently on a battery of trained, visual form discriminations.

METHOD

Animals

Six cats were used, all of them cage-reared in the laboratory from an age of seven weeks or younger. At the start of the experiment they ranged in age from six to ten months, and previously had had no experience with any sort of formal learning. They were maintained in open wire cages (approximately 60 by 75 by 90 cm.).

Preoperative Training

The cats were taught to perform a series of pattern or contour discriminations by methods described earlier (4). Training was carried out in a darkened discrimination box in which the translucent patterns to be discriminated were presented in two swinging doors at the end of the box which the cats pushed open with their heads. A correct choice allowed access to a morsel of food; an incorrect choice activated an electric buzzer. The cats were trained to discriminate an equilateral triangle from any of a series of imperfect triangles of similar dimensions arranged on a scale in which the critical difference was gradually reduced, as shown in Figure 1. Simultaneous paired presentation of positive and negative patterns was used with cats *Slp*, *Whs*, *Nsy*, and *Sst*. With cases *Nbr* and *Clv* individual successive presentation was employed as described below.

As a rule 30 to 50 trials were run per day, all on the same kind of negative pattern. The daily sessions were started with 1 to 5 runs on each of the simpler stages of the pattern already mastered and proceeded to more difficult stages as rapidly as learning permitted. The most difficult or "top" negative figure that could be discriminated was determined prior to operation for each type of negative pattern. The discrimination habits were stabilized by overtraining approximately 400 trials on figures of intermediate and high difficulty. The training and overtraining schedules were interrupted erratically and extended over prolonged periods totaling 5 to 18 months.

Surgery

The cats were anesthetized with veterinary Nembutal (intraperitoneal injection of 38 mg. per kg. body weight). The skull was opened on both sides and across the mid-line with a dental crown saw and rongeurs until a wide bilateral exposure of the visual cortex was achieved. Small plates of mica (0.02 to 0.04 mm. thick, 2 to 4 mm. wide, 3 to 20 mm. long, and slightly pointed at one end to facilitate insertion) were then pushed into the visual region in the over-all patterns shown in Figure 2. The mica was inserted through short slits in the pia that were cut in advance with a fine steel knife. The majority of plates were individually trimmed in length and width at the time of insertion to suit the locus of implantation. An attempt was made to avoid interrupting the optic radiations as much as possible by placing the deeper insertions in a plane parallel with the radiation fibers. The larger blood vessels on the surface were avoided, but there was extensive hemorrhage in many instances from large unseen vessels running deep in the fissures. The dura was replaced over the implants and fastened with fine silk sutures. A median bridge of the skull plate 1.5 to 2.0 cm. wide was reinserted over the saggital sinus and fastened firmly with tantalum sutures. Penicillin (procaine G, 300,000 units) was injected intramuscularly at the start of the operation and on the following four days.

Postoperative Testing

Fifteen to 27 days were allowed for recovery from the surgery. The tests were started with figures that

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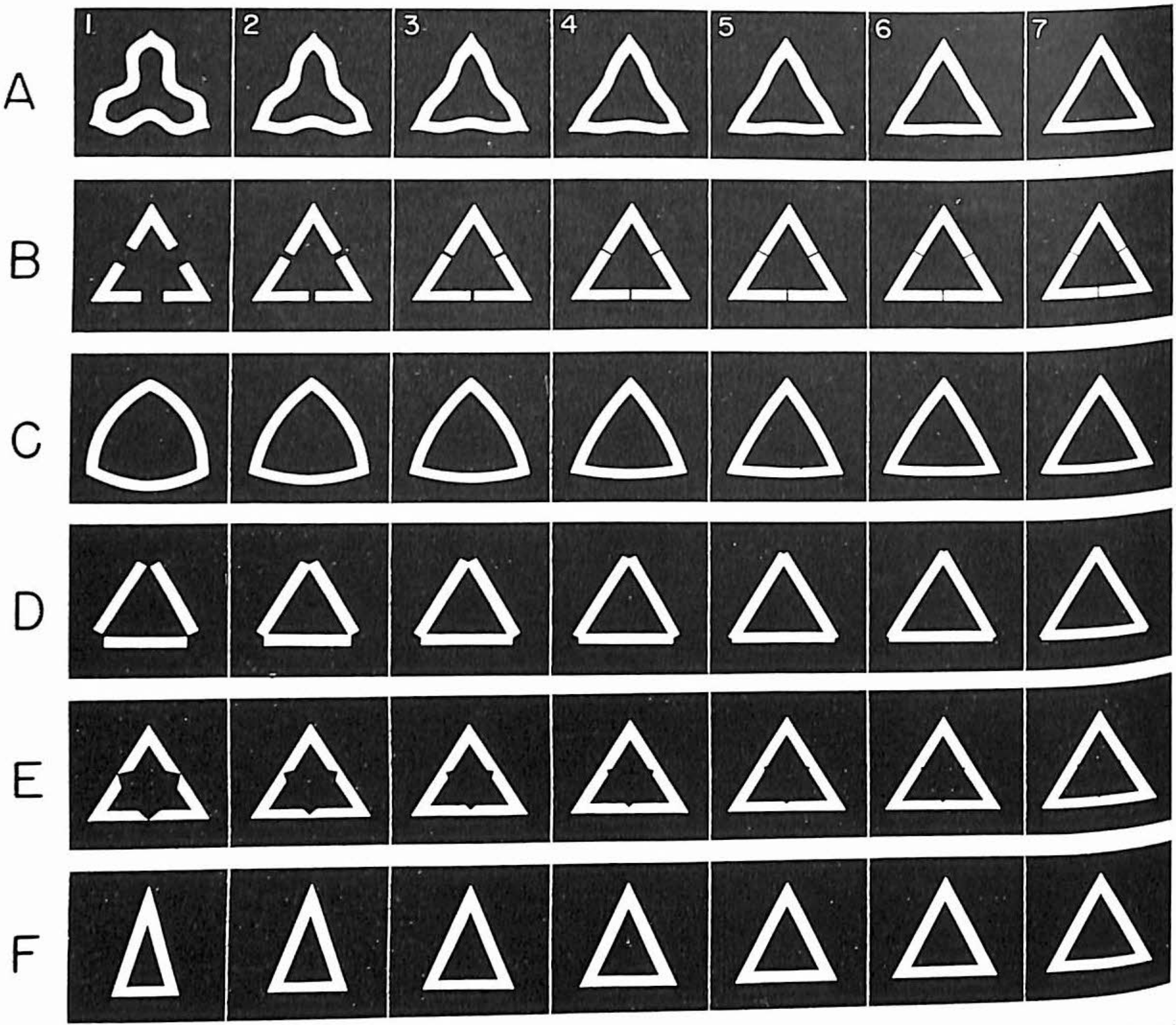

FIG. 1. Test scale of the negative figures reproduced from photostats of original stimulus cards. Positive figure was always an equilateral triangle like B7 without the crosslines.

were arbitrarily selected in each case according to the apparent degree of recovery as judged on the basis of generalized visual behavior. The test figures were then adjusted immediately upward or downward on the scale depending on the performance until the most difficult figure that could be discriminated was determined for each pattern. Only one type of negative pattern was tested on a given day. A performance level of 16 or more correct out of 20 consecutive trials was used as the criterion of discrimination. In all but one case, *Slp*, the postoperative testing extended over periods of three to six and one half months. Tests were carried out at arbitrary intervals during this time with lay-offs not longer than six weeks, an effort being made to keep the tests frequent enough to avoid regressions from loss of memory.

Follow-up Examination

After the brains had been fixed by perfusion with 10 per cent formalin, they were removed, photographed, and X-rayed to record the pattern of mica inserts. The mica pieces were then pulled out and measured. The brains were dissected carefully to assess better the extent of the damage and degeneration, particularly that in the white matter. The lateral geniculate nuclei were excised, sectioned transversely at 25 mu, and stained with cresyl violet to determine the amount of retrograde degeneration caused by interruption of the optic radiation fibers.

OBSERVATIONS AND RESULTS

Mica Implants Limited Mainly to Cortical Gray, Case Slp

This first cat was trained on our earlier test scale (4) to the highest level on A through F with approximately 475 overtraining trials on each top figure. Mica plates were then inserted bilaterally, as shown in Figure 2. An attempt was made to confine the mica implants to the gray matter, avoiding damage to the underlying white matter as much as possible, particularly in the critical area of central vision.

Slp was nearly blind on the third day after operation, but vision returned rapidly during the following week until on day 12 it seemed nearly normal to casual observation. Postoperative testing was started on the fifteenth day after operation. In the first 20 trials on each figure, *Slp* discriminated all its most difficult test figures except A4 and E4. In a second 20 trials on these latter patterns, *S* succeeded with A3 and E3.

Implants Invading White Matter

After observing the high-level postoperative performance of the first case, we proceeded to make the implantations more drastic. The over-all pattern of inserts was much the same, but larger numbers of mica plates were implanted, and they were inserted deeper. The resultant invasion of the white matter along with the additional cortical damage in the remaining four experimental cases produced a moderate to severe impairment of vision that persisted beyond the early ten-day period of edema and inflammation. Improvement in vision was fairly rapid during the first weeks after operation, tending to taper off gradually thereafter to a final level that varied with the severity of cerebral insult. All the remaining cases were trained and tested in an improved discrimination box with the battery of test figures illustrated in Figure 1. The postoperative performances tabulated below include the

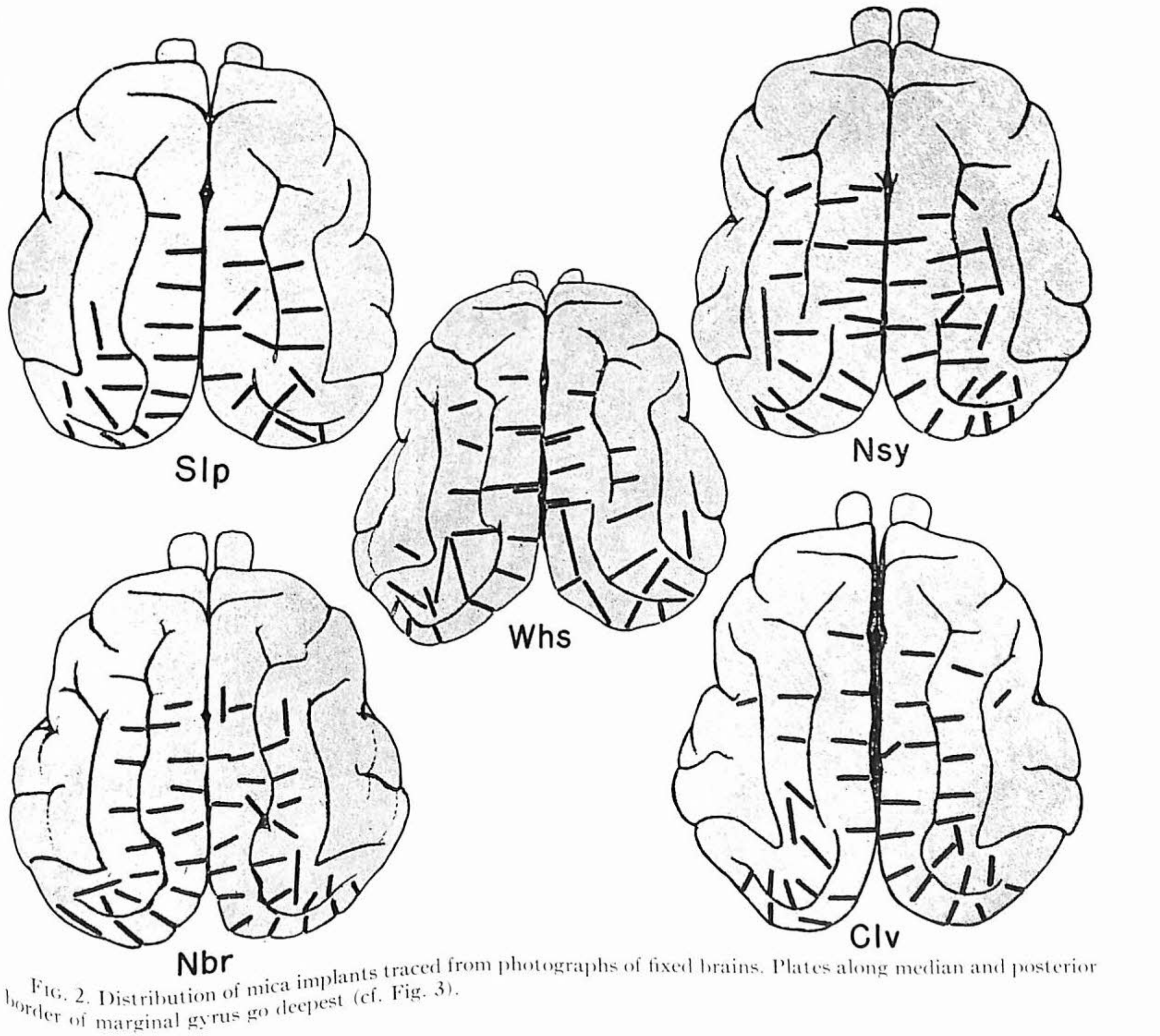

FIG. 2. Distribution of mica implants traced from photographs of fixed brains. Plates along median and posterior border of marginal gyrus go deepest (cf. Fig. 3).

best achievements of the first several days of postoperative testing for each pattern and also the most difficult (top) figures mastered later after recovery had reached a stable level.

Simultaneous Presentation, Cases Whs and Nsy

As shown in Tables 1 and 2, *Whs* eventually attained a high level of recovery, mastering most of its top preoperative patterns, whereas *Nsy* did less well. The difference was partly reflected in the amount of brain damage in the two cases, but other factors were involved. *Nsy* had never performed as well as *Whs* even before operation. During surgery, widespread yellowish granulations were noted in the pia-arachnoid of *Nsy*, suggestive of an earlier meningitis. Two weeks after surgery the scalp had to be reopened to drain a suppurative infection which gradually subsided under penicillin treatment. At nine weeks another ulceration broke through the scalp. When the brain was removed 15 weeks after operation, widespread infection was evident under the skin extending into the brain at several points around the mica. Because of the complications in *Nsy*, the performance of *Whs* was regarded as the more informative of the two cases.

TABLE 1

Summary of Case *Whs*

Preoperative			Postoperative			
Overtrained			Initial Discrimination		Top Figure Achieved	
No. of trials	Fig.	Top fig. achieved	Fig.	Days postop.	Fig.	Days postop.
446	A4	A7	A3	27	A7	114
426	B6	B7	B4	35	B6	74
420	C6	C7	C5	32	C7	61
400	D6	D7	D6	42	D7	73
800	E6	E7	E5	47	E6	61
424	F6	F7	F5	34	F7	52

TABLE 2

Summary of Case *Nsy*

Preoperative			Postoperative			
Overtrained			Initial Discrimination		Top Figure Achieved	
No. of trials	Fig.	Top fig. achieved	Fig.	Days postop.	Fig.	Days postop.
410	A4	A6	A1	29	A3	64
190	B6	B6	B1	27	B3	80
205	C4	C5	C2	35	C4	72
420	D4	D5	D1	45	D1	45
325	E4	E5	failed E1	48	E1	83
240	F4	F5	failed F1	37	F2	77

TABLE 3

Summary of Case *Nbr*

Preoperative			Postoperative			
Overtrained			Initial Discrimination		Top Figure Achieved	
No. of trials	Fig.	Top fig. achieved	Fig.	Days postop.	Fig.	Days postop.
360	A3	A4	A3	22	A4	87
350	B5	B6	B2	20	B3	73
500	C4	C6	C4	23	C4	23
375	D2	D3	D2	24	D3	85
400	E3	E5	E1	27	E2	61

TABLE 4

Summary of Case *Clv*

Preoperative			Postoperative			
Overtrained			Initial Discrimination		Top Figure Achieved*	
No. of trials	Fig.	Top fig. achieved	Fig.	Days postop.	Fig.	Days postop.
445	A3	A4	A1	27	A2	125
660	B4	B5	B2	44	B2	44
675	C3	C5	failed C1	41	C5	129
550	D2	D5	failed D1	42	D3	120
420	E3	E5	failed E1	45	—	—

* When retrained during the sixth month after operation, and allowed to compare negative and positive figures simultaneously like *Slp*, *Whs*, and *Nsy*, *Clv* successfully discriminated figures A3, B2, C5, D4, and E2.

Serial Presentation, Cases Nbr and Clv

The last two cats were trained to perform a more difficult type of discrimination in which only one test figure was presented at a time. The cat had to respond differentially depending on whether the figure shown was the positive equilateral triangle or one of the imperfect negative triangles. Both positive and negative figures were presented in the right door of the training box. When the positive figure appeared, the cat approached it and pushed open the door. When a negative figure was presented, the cat avoided it and went instead to the left door, marked only by a vertical slit of light that remained constant. It was thought that this use of a single figure constituted a somewhat more critical test of possible perceptual distortions. In part it was an answer to an earlier objection (4) that with two figures, both might be distorted and yet still be distinguishable because the positive would be less distorted than the negative.

As seen in the tables, the general level of performance, both pre- and postoperative, was lower throughout on this more difficult task. The F series was abandoned because the training proved too difficult under these conditions. The postoperative performance of *Nbr* was somewhat better than that of *Clv*, and this correlated with the degree of cerebral damage produced by the mica inserts.

Knife Cuts Without Mica, Control Case Sst

In a sixth cat deep knife cuts were made in the same general pattern as the mica implants. The cuts went well down into the white matter, simulating the tissue damage produced by the more drastic of the mica implantations. Nothing was inserted into the cuts, the aim being to find out to what extent the functional impairment in the experimental cases might be ascribed to the dielectric properties of the mica and how much to the tissue injury alone. The resultant impairment proved to be as great as in the most severely affected of the experimental group. Trained preoperatively to discriminate A4, B5, C4, and F4, with a minimum of 300 overtraining trials on each, the best *Sst* could do at six weeks after opera-

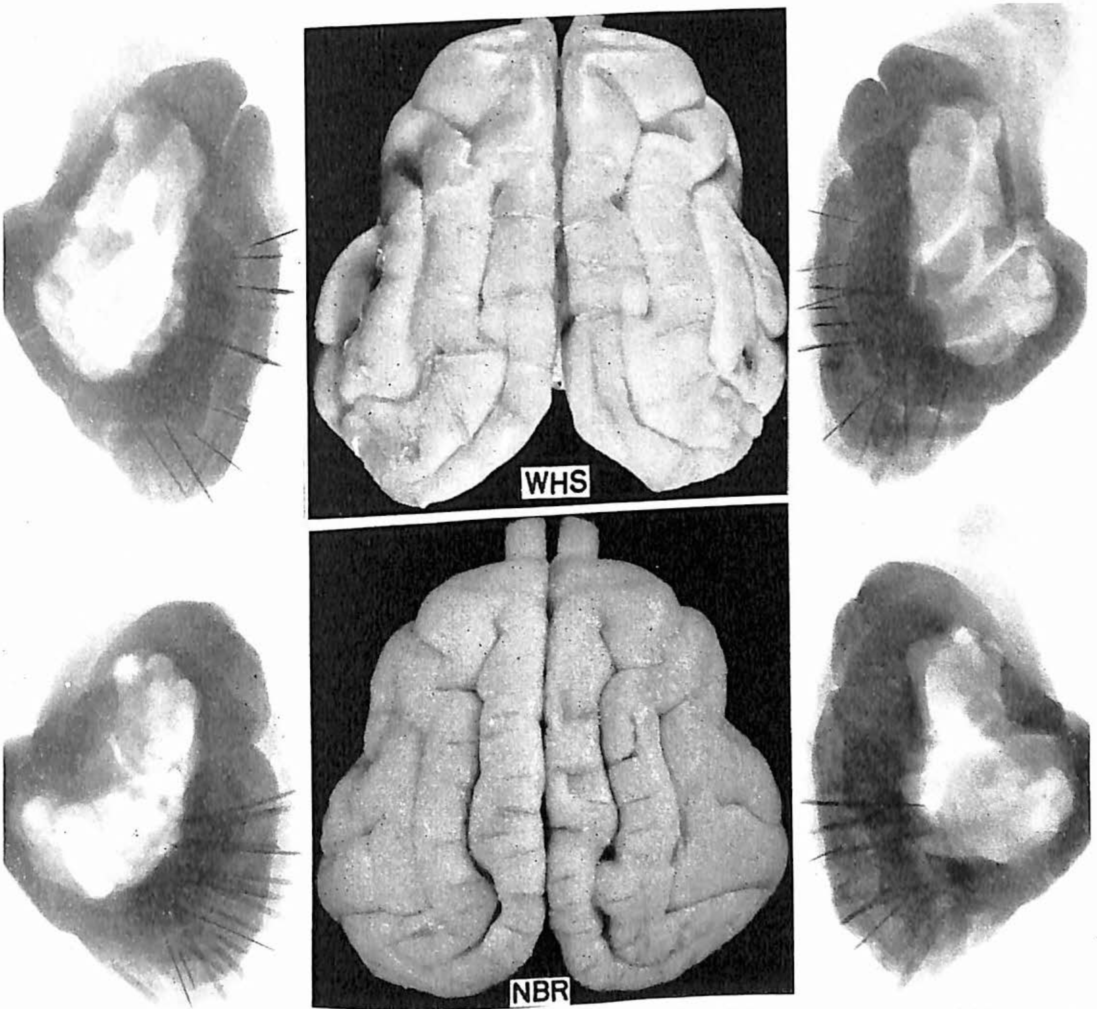

FIG. 3. Surface and X-ray views of fixed brains of *Whs* and *Nbr*. Not all inserted plates are visible at surface. X-ray views show only thicker of mica plates and/or those viewed edgewise.

tion was A1 and F1. It failed repeatedly to make criterion on B1 and C1.

POST-MORTEM INSPECTION OF BRAINS

The mica plates were found to have survived in good condition in all cases without deterioration or crumbling. In the four cats retained for testing longer than three months after operation the mica implants had become encased in thick connective tissue sheaths that must have further enhanced their current distorting properties. The extent of damage to the cortical gray itself can be estimated roughly from Figures 2 and 3.[2] The nature and general pattern of the cortical lesions was much the same in all cases, and the amount of damage to the cortex was roughly of the same order.

Much greater variation was found in the extent to which the inserts had invaded and damaged the white matter. Invasion of the white was least in *Slp*. The medial portion of the white in the splenial, suprasplenial, and fornicate gyri was divided in *Slp*, and the plates invaded approximately the upper third of the white in the marginal and suprasylvian gyri. In the other four experimental cases, the splenial, suprasplenial, and fornicate gyri were almost completely divided by many of the inserts, and on the lateral surface most of the implants extended all the way to the base of the white in the suprasylvian and marginal gyri. In general the implants went deeper than had been intended—a result of the improvised trimming of the mica plates without close measurement during the surgery. In all cases two or more implants penetrated the lateral ventricle on each side. In *Whs* the two deepest plates on each side pierced the hippocampus. In *Nbr* seven implants had penetrated the ventricle on the left side and three on the right side. When the mica plates were extracted, the degeneration in the surrounding tissue varied from being hardly noticeable to the extent of producing large oval cavities 2 by 3 mm. Among the four cases, damage to the white was least in *Whs* and greatest in *Nsy* and *Clv*.

The geniculate bodies of all cases but *Slp* were sectioned and examined microscopically. They showed varying degrees of degeneration scattered irregularly through the nucleus. Rough estimates of the total percentage of reduction of principal cells in the dorsal nucleus on the side least impaired ranged from around 10 per cent in *Whs* to 20 per cent in *Nbr*, 50 per cent in *Clv*, and 75 per cent in *Nsy*. Fibers to the critical area of central vision appeared to have suffered greatest in cases *Nsy* and *Clv* and were best preserved in *Whs*.

In the control case the invasion of the white matter approached that found in *Nsy* and *Clv*. In particular, the optic radiations on both sides were invaded by cuts in the region for central vision. Correlated with this, extensive degeneration was evident in the lateral geniculate nucleus amounting to roughly 80 to 85 per cent.

DISCUSSION

The functional effects of mica implantation appeared to reflect throughout the amount of tissue damage incurred rather than the degree or quality of electric current disturbance. The distorting influence on the mass "figural" currents within the cortical gray itself should have been roughly of the same order in all five experimental cases. According to the electric field hypothesis (1), the distortion of relational effects mediated by mass current flow should have been sufficient to cause drastic disruptions of pattern perception. The high-level postoperative performances of *Slp*, *Whs*, and *Nbr* speak strongly against electric field theory as currently conceived.

Although the cortical destruction was roughly similar in the different cases, that to the underlying white matter varied over a considerable range and was correlated with the degree of functional impairment. As in the sensorimotor cortex of the monkey (3), knife cuts entering the white matter tended to have much more severe effects on function than cuts confined to the gray. The poor scores of the control case taken in conjunction with the earlier results on subpial slicing (4) support further the inference that the functional deficits were produced by the tissue lesions per se, particularly those to the white, and not by the dielectric properties of the mica inserts.

Relearning may have been partly responsible for the gradual improvement that followed the initial postoperative performance in the four cases that were tested over a long recovery period. Probably a more important factor was the spontaneous recovery from a state of cerebral depression or shock (diaschisis) produced by the surgical trauma. This is suggested in the observation that improvements continued to take place during lay-off periods when the cats were not being run, particularly during the first six weeks after operation.

The presence of relearning would not in itself invalidate the above conclusions unless the cats had learned to recognize and discriminate illusory distortions produced by the mica. If the distortion of cortical currents had in fact caused corresponding distortions in the perceptual appearance of the stimulus figures as conceived in electric field theory (1), the distortion patterns should have differed markedly for each fixation point of the eyes in looking at the figures. Any single figure would have assumed a different and grossly distorted shape for each new fixation point. Furthermore, eye and head movements made while viewing the figures should have resulted in a violent writhing, splintering, and shimmering of the test figures. It is difficult to believe that the high-level postoperative discriminations of *Whs* and *Nbr* in particular could have been achieved under such conditions. Moreover, in the case of *Slp* there was no opportunity for relearning.

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[2] The X ray pictures were taken by Dr. R. S. Harrison, Huntington Memorial Hospital, Pasadena.

The results seem best accounted for on the assumption that the mica implants produced (*a*) scotomata of varying size and shape correlated with the location, size, and shape of the lesions, plus (*b*) a generalized and partly reversible traumatic depression of the remaining structures with which the destroyed cells and fibers were associated, and possibly (*c*) certain perceptual disturbances (like micropsia, macropsia, displacements, polyopia) as described by human patients with occipital lobe injuries (5). The cats, like human patients, may have remained largely or entirely unaware of the widely scattered scotomata, and their postoperative perception may have been aided by a tendency for perceived figures to be completed across the blind areas. If the implants produced disturbances that reached awareness as listed under (*c*), these latter were not sufficiently marked to prevent pattern recognition at fairly high levels.

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INTEROCULAR TRANSFER OF PATTERN DISCRIMINATION IN CATS FOLLOWING SECTION OF CROSSED OPTIC FIBERS[1]

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In an early investigation it was found that pigeons fail to retain with one eye object discrimination habits learned with the other eye (1, 2). In subsequent studies, however, brightness and form discriminations have been observed to transfer from one eye to the other in chick and pigeon, respectively (4, 9). The discrepancy seems to have been resolved by further investigations with the pigeon which indicate that the occurrence of interocular transfer depends upon the locus of the stimulus figures within the visual field during the training and testing procedures (5, 6, 7). Interocular transfer of learned discriminations has been demonstrated also in teleost fishes (8, 10).

In these submammalian forms in which there is complete decussation of retinal fibers in the optic chiasma, the presence of interocular transfer implies an interaction between the two brain-halves at a fairly high level of organization. Interocular transfer in mammals has a quite different significance, owing to the bilateral projection of the afferent fibers from each eye. However, a related type of interaction between the two sides of the brain may be studied in the mammal if one first divides the crossed optic fibers in the chiasma. In the absence of the crossed fibers, the patterns of stimulation from each retina are conveyed entirely to the ipsilateral brain-halves by the remaining uncrossed fibers. The present paper deals with tests for interocular transfer of pattern and contour discrimination under these conditions in the cat.

METHOD

Animals

Nine cats were used, all of them cage-reared in the laboratory from an age of six weeks or younger. They ranged from five to nine months in age at the time they were used in the present experiment. Prior to this time the cats had had no experience with the experimental test patterns nor with any sort of formal visual learning. They had been outside of their cages (open wire, approximately 60 by 75 by 90 cm. in size) only for short intervals during the daily cleaning of the cages.

Surgery

The optic chiasma was transected in the mid-sagittal plane through a transbuccal approach. In this procedure the soft palate was incised from its attachment to the hard palate anteriorly to within a half-centimeter of its free margin posteriorly. The cut edges were retracted with catgut sutures creating a diamond-shaped opening. A flap of nasal mucosa was next reflected from the sphenoid bone, and, with a dental burr, an oval fenestra 4 by 5 mm. was made in the bone immediately anterior to the spheno-presphenoidal suture. Through this opening in the bone the dura was carefully exposed and incised, thus revealing the underlying optic chiasma. The chiasma was then sectioned with a fine steel blade under close visual control through a binocular dissecting microscope. A small piece of tantalum foil was inserted between the cut halves of the chiasma so that postmortem verification of the completeness of section would be possible by gross inspection.

After section of the chiasma, the opening in the bone was filled with Gelfoam soaked in blood to form a barrier between the nasopharynx and cranial cavity. The flap of mucosa was replaced over the Gelfoam and the incised soft palate reapposed with catgut sutures.

The anesthetic for all operations was pentobarbital sodium (38 mg. per kg. body weight, intraperitoneal). Procaine penicillin G (300,000 units) was injected intramuscularly on alternate days for one week following surgery to combat meningeal infection. At the end of the experiment, a lethal dose of pentobarbital sodium was administered. The brains were fixed by perfusion with 10 per cent formalin and checked for remaining crossed optic fibers.

Training and Testing

Three weeks were allowed for recovery before training was started. The pattern discriminations were taught in a training box (see 11, 12) in which the two patterns to be distinguished were presented side by side in two swinging doors which the cats pushed open with their heads. A correct choice allowed access to a morsel of food; an incorrect choice activated an electric buzzer. The cat was trained to return in either case to the starting chamber for the next trial. The five pairs of test patterns that were used are illustrated in Figure 1. The patterns of each pair were constructed of equal surface area. The right-left position was alternated according to Gellermann's principles (3).

Light was excluded from one eye throughout the training and testing by the use of a black rubber mask held tightly in place by ties to a leather collar. Since measurement of learning rate was not of primary concern, the cats were run to satiation each day during the training periods. To facilitate learning, the positive pattern was lighted more brightly in the beginning, and as learning progressed, the light difference was gradually eliminated. When the cats attained a performance level of 34 or more correct in 40 trials after the patterns had been equated for brightness, the discrimination was stabilized by overtraining with 40 trials a day. The total number of overtraining trials for each discrimination is listed in Table 1. Where two discriminations were taught, one to each eye (as with *Bgw*, *css*, *Sll*, and *Brn*), the final 280 to 320 overtraining trials on both were carried out concurrently, i.e., on odd days 40 trials were run with one discrimination, and on the even days 40 trials were run with the second discrimination. Cat *Bsh* subsequently learned a third discrimination. Tests for interocular transfer of a given discrimination were carried out by placing the mask over the eye used in learning that discrimination and presenting the patterns to the "untrained" eye for 40 test trial runs.

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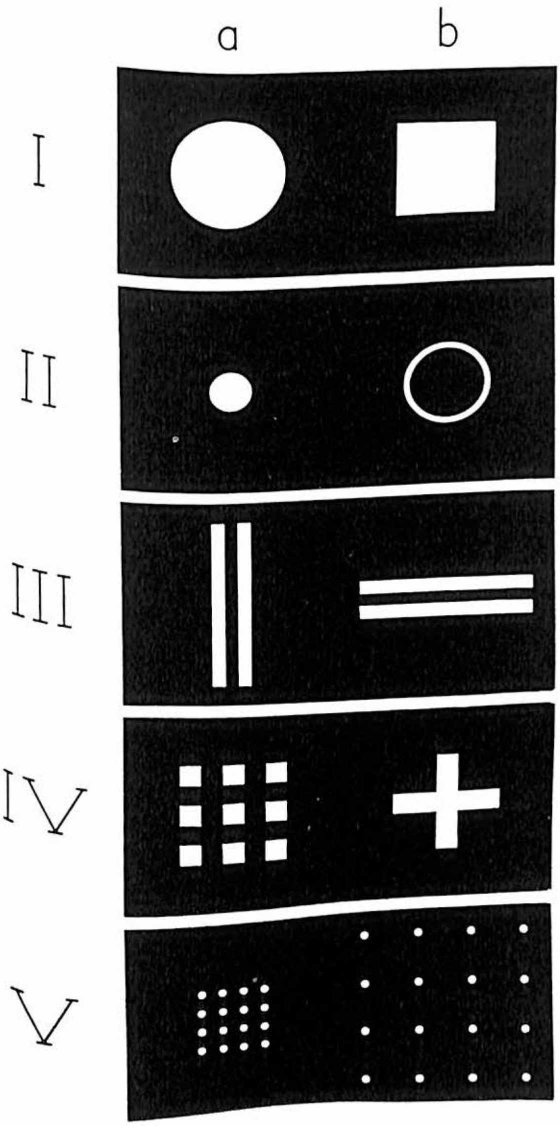

FIG. 1. Pairs of test patterns. Cats were trained to select patterns in column *a*. No initial preference for patterns in either *a* or *b* was evident.

TABLE 1

Level of Interocular Transfer

Cat	Eye Trained	Test Patterns	Number of Over-training Trials	Av. No. Correct Out of 40 on Final 120 Over-training Trials	No. Correct on 40 Critical Trials with Untrained Eye
Mmm	R	I	120	39.0	38
Bgw	L	III	400	39.7	39
	R	II	440	38.3	37
Css	L	II	440	38.7	33
	R	III	440	40.0	39
Bsh	L	III	240	40.0	39
	R	IV	440	39.7	27
	R	II	560	35.7	34
Sll	R	III*	400	40.0	34
	L	V	400	40.0	39
Brn	R	III	400	39.7	38
	L	IV	440	39.3	30
Kns	R	IV	400	39.0	21
Pll	R	II	400	38.3	34
Hrl	R	IV	160	38.3	35

* This one case was trained to choose the horizontal lines in III instead of the vertical.

RESULTS

Although aided during training by differential lighting of the figures, and occasionally by other measures such as leaving the correct door ajar, the cats required roughly 330 to 1,250 trials in from 4 to 21 days to learn their first discrimination problem. The second and third discriminations, learned after the animals had become accustomed to the training procedure, required 240 to 385 trials in 4 to 8 days. The cats' discriminative capacity was lowered under the conditions of the experiment necessitating the use of relatively simple test patterns.

The scores obtained with the untrained eye along with the relevant data are summarized in Table 1. It can be seen that for 14 of the 15 discrimination habits tested, the level of performance with the untrained eye was 27 or more correct choices in the 40 critical trial runs. The probability of an animal's obtaining a score of 27 or more correct on a chance basis is less than five in a hundred In 11 of these 15 habits the performance was 34 or more correct, the probability in this case being less than one in a thousand.

In the single exceptional case, *Kns*, the performance level on the tests for transfer of habit IV approached chance. The records show a reversion to a position response. On the following day, when retested with the trained eye, *Kns* performed 39 correct out of 40. On the third day a second 40 trials were run with the untrained eye and with the reward–punishment value of the two patterns interchanged. This time the cat chose the pattern that had originally been positive 29 times out of the 40 despite its then being associated with punishment. Some transfer effect was thus evident from the second 40 trials. This latter score could not be ascribed to relearning in view of the reward–punishment reversal. A similar observation has been reported by Levine (6) with pigeons.

The completeness of the chiasma section was readily verified by gross inspection of the fixed brains in all cases except *Mmm* and *Bgw*. In these two the completeness of section was satisfactorily confirmed by histological examination.

DISCUSSION

It is evident from the general high level of performance on the critical trial runs with the untrained eye that pattern discriminations learned with one eye can be performed with the other by cats in which all crossed optic fibers have been sectioned. The high-level performance with the untrained eye could hardly be ascribed to rapid learning. In four of the habits tested, as few as one mistake was made on the 40 critical trial runs, and one animal made this single mistake as late as the twenty-eighth trial.

In all cases the performance was somewhat better with the trained than with the untrained eye, indicating that the trained and untrained sides are not completely equivalent. This difference was more pronounced with test patterns II, which were relatively difficult, than with the easier patterns of III (criteria of difficulty being the learning rate and the final level of performance on the overtraining trials).

It is of interest to note that the exceptionally low level of transfer obtained in *Bsh* and *Brn* occurred in both cases with test patterns IV. Further, the second eye of both cats had previously been trained to discriminate the patterns of III. Inspection of the two sets of patterns (see Fig. 1) suggests the possibility that the low level of transfer in these two cases was caused by interference effects arising from similarities between the two sets of patterns.

SUMMARY

The afferent connections from each eye were restricted to the ipsilateral brain-half in nine cats by surgical section of the crossed fibers in the optic chiasma. The cats were then trained to perform pattern discriminations with a mask covering one eye. When the mask was later shifted to the opposite eye, it was found that the discriminations could be performed correctly with the untrained eye. The results illustrate a type of functional equivalence and an integration of considerable complexity between the visual mechanisms on the two sides of the brain.

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CERTAIN DIFFERENTIAL EFFECTS OF LEFT AND RIGHT CEREBRAL LESIONS IN HUMAN ADULTS[1]

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An interesting symptom-aggregate attributed to lesions in the right parietal lobe in human beings has recently been described by Brain (2), Critchley (5), and Denny-Brown, *et al.* (6). The primary defects appear to be a loss in the significance of stimuli (particularly visual, but also auditory and tactile) in the left side of extrapersonal space, dressing dyspraxia, and construction defects approaching or at least simulating construction dyspraxia. Each of these defects would appear to represent a difficulty in manipulating, ordering, or effecting spatial relationships.

Birren (1) and Cohen (3) have recently published independent factorial analyses of the Wechsler-Bellevue Scale based upon groups which differed with respect to age as well as psychiatric and neurologic diagnoses. In each solution, significant loadings were contributed by the same subtests for the first two factors extracted. One of the factors was composed of only verbal subtests and the other of only performance subtests. The factors were called "Verbal Comprehension and Closure" by Birren, and "Verbal and Nonverbal Organization" by Cohen.

The left (so-called dominant) hemisphere in right-handed people has been associated with language functions since 1836, when Marc Dax published his observation that speech impairment is much more frequently associated with right than left hemiplegia. The right parietal lobe may subserve abilities in spatial organization as suggested by Brain, Critchley, and Denny-Brown. Judging from a patient described by Hebb (8), with a lesion attributed to the right temporal lobe, the possibility exists that in some instances organizational abilities may be subserved by the right temporal lobe as well. These reports suggested the hypothesis that lesions in the right cerebral hemisphere might impair ability on the performance subtests of the W-B, and the lesions in the left hemisphere might lower the scores on the verbal subtests. An attempt was made in this study to perform a preliminary test of this hypothesis.

METHOD

Subjects

One group was composed of 14 patients with lesions of the left hemisphere and another of 17 patients with right cerebral lesions. The hemisphere involved in each patient was verified at surgery. These patients represented all admissions, during a two-year period, who had received psychological tests and who, in addition, were classified as having unilateral cerebral lesions. The neurological examination and diagnostic procedures preceding surgery were completely independent of the psychological testing both with respect to the examiners involved and technique used. The diagnostic procedures included complete neurological examinations, electroencephalography, and cerebral angiography and/or air studies. The psychological examiner was completely unaware of these results prior to administration and scoring of the tests.

No attempt was made to select patients with involvement in one or another lobe of the hemisphere damaged. The groups were not composed in such a way that results would be of significance with respect to localization of brain functions, since the sites of primary involvement for individual patients included all the lobes in each group. Only lateralization of functions was investigated in this study.

In spite of the care used to select patients with unilateral lesions, it was impossible to rule out completely such influences on the supposedly normal hemisphere as intracranial hypertension, edema, and impaired vascularization. Post-mortem examinations were not obtained, and thus the possibility of bilateral involvement being present in some patients is by no means ruled out. Such occurrences, however, should decrease the differences in the groups and thus tend to minimize the probability of obtaining significant results.

A third group consisted of 31 patients with generalized brain damage, and included diagnoses of general paresis, multiple sclerosis, congenital brain anomalies, degenerative cerebrovascular disease, and traumatic head injuries. Patients with traumatic injuries were included in this third group regardless of the site of focal damage, because of the strong likelihood of diffuse as well as focal damage in these patients (4).

The patients were tested after they had received maximal benefits from hospitalization and were ready for discharge. Eight of the 14 patients with lesions in the left hemisphere, however, had mild dysphasia at the time of testing. None was severely handicapped in verbal expression. All patients included in the study were right-handed.

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Although insufficient patient material prohibited individual matching of patients on control variables such as sex, age, education, etc., the group means were fairly similar for age and education. Means for chronological years of age were: left-sided damage, 40.21; right-sided damage, 39.59; and diffuse damage, 36.10. Means for number of years of formal education were: left-sided damage, 11.14; right-sided damage, 10.65; and diffuse damage, 10.58. None of these mean differences approached statistical significance.

Procedure

A wide variety of tests was administered to each patient, including the Wechsler-Bellevue Scale (Form I), the tests proposed by Halstead (7) for measuring biological intelligence, the Minnesota Multiphasic Personality Inventory, and the Halstead-Wepman Aphasia Screening Test. Only the results of the Wechsler-Bellevue Scale were selected for analysis in this study.

The Wechsler-Bellevue Scale was administered to each patient by a person other than the writer who was trained in administration and scoring in accordance with Wechsler's standards. The tests for all patients were scored finally before the groups were composed. Means and standard deviations were calculated and differences between group means compared statistically. Spearman rank-difference correlations were calculated for subtest rank order in the groups.

RESULTS

Mean weighted scores on the Wechsler-Bellevue subtests are shown for each group in Figure 1.

On each of the verbal subtests the group with lesions of the left hemisphere had the lowest means. On the performance subtests, however, the group with lesions of the right hemisphere consistently had the lowest mean scores. The group with diffuse brain damage roughly approximated the group with lesions of the right hemisphere on the verbal subtests and the group with lesions of the left hemisphere on the performance subtests. Differences between the level of ability shown on the verbal and performance subtests is indicated by the fact that the group with left-sided lesions had a verbal weighted-score average about 12 points below the performance weighted-score mean. The group with lesions of the right hemisphere had a difference of 11 points in favor of the verbal over the performance weighted-score mean. The group with diffuse involvement had verbal and performance weighted-score means differing by only 1 point.

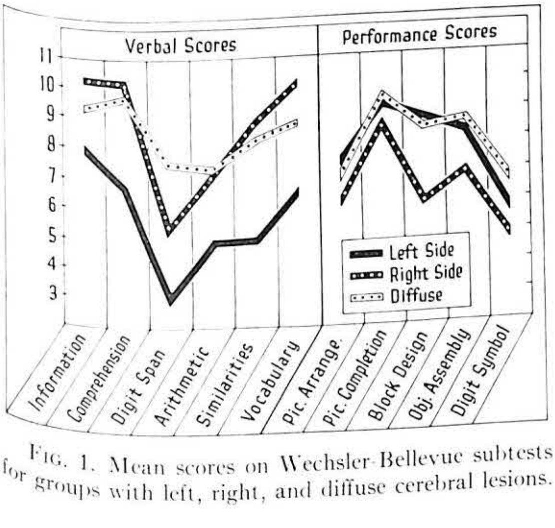

FIG. 1. Mean scores on Wechsler-Bellevue subtests for groups with left, right, and diffuse cerebral lesions.

The consistency with which the differences were shown is indicated by the finding that 13 of the 14 patients with left cerebral lesions had lower verbal than performance total weighted scores. Fifteen of the 17 patients with lesions of the right hemisphere, however, had higher verbal than performance weighted-score totals. In the group of 31 patients with diffuse damage, 17 had higher verbal than performance totals, 12 higher performance than verbal totals, and 2 had equal verbal and performance totals.

The mean values for the three brain-damaged groups were compared statistically. These results are presented in Table 1.

Values of 2.75 and 2.04 are needed in the right- versus left-sided comparisons to reach the .01 and .05 levels of confidence, respectively. In the diffuse versus left- and diffuse versus right-sided comparisons, values of 2.70 and 2.02 are necessary.

The differences between means for the group with right and the group with left cerebral lesions were significant at the .05 level or beyond for each of the verbal subtests except arithmetic. The Verbal Standard Score and Verbal IQ means were also significantly different. Each difference was in the same direction, the right-sided group having the higher mean values.

Although the left-sided group had higher means on each performance subtest, no difference was large enough with relation to the variability of scores to reach the .05 level. In consideration of these results it would seem legitimate to suggest that patients with right-

TABLE 1

Comparison of Mean Wechsler-Bellevue Scores by t Ratios for Diagnostic Groups

	Inf	Comp	Dig Span	Arith	Simil	Voc	Pict Arr	Pict Comp
Right vs. Left	2.07	2.59	2.45	1.47	2.95	2.81	.89	.45
Diffuse vs. Left	1.32	2.52	4.52	1.94	2.93	2.10	.36	.35
Diffuse vs. Right	1.16	.53	2.38	.12	.62	1.60	.82	.94

	Block Design	Obj Assem	Dig Symb	VWS	PWS	TWS	VIQ	PIQ	TIQ
Right vs. Left	2.03	.85	.79	2.58	1.21	.73	2.44	1.34	.65
Diffuse vs. Left	.34	.37	.98	3.34	.26	2.13	2.96	.42	1.60
Diffuse vs. Right	2.03	1.61	1.93	.00	1.73	.98	.21	1.34	1.50

and left-sided cerebral injuries represent different populations among brain-damaged *S*s.

The group with diffuse involvement significantly excelled the left-sided group on all verbal subtests except Arithmetic and Information. Only Digit Span and Block Design reach the .05 level in the diffuse versus right-sided comparisons, with the diffuse group having the higher mean in each instance. The results indicate that the group with right-sided damage was a good deal more similar to the diffuse group than were the patients with left cerebral damage.

As an additional comparison, Spearman rank-difference correlations between the rank order of subtest means in the three groups were computed. A coefficient of .75 was obtained between the group with diffuse damage and the one with right cerebral lesions. The correlation between the groups with diffuse and left cerebral lesions was .53. The groups with unilateral lesions, however, had a coefficient of only .17. These results indicate that our group with diffuse damage was fairly similar in this respect to the groups with unilateral lesions, but that the latter groups differed considerably. As an example of this, the Block Design subtest had the second highest mean of the 11 subtests for the group with left cerebral lesions, but the third lowest for the group with right cerebral lesions. Similarities had the fourth highest mean for the group with right cerebral damage, but the third lowest for the group with lesions of the left hemisphere.

DISCUSSION

While the results suggest a differentiation of measured abilities subserved by the two hemispheres, a question may be posed concerning the possibility of more precise localization. This is a question which we have made no attempt to answer with our present findings. The widespread, microscopically observable effects of intrinsic brain lesions in clinical human material makes the problem of localization extremely difficult. Even with structurally discrete intrinsic lesions, the occurrence of vascular changes and edema may be widespread in the hemisphere.

The impaired performance on verbal subtests for the group with lesions of the left hemisphere may be associated with organic language loss, since 8 of the 14 patients had mild residual dysphasia. If this is true, it is difficult to say whether the verbal scores represent an impairment in intelligence or, to use Goldstein's term, a defect in the "instrumentalities of speech." An unresolved question has long been debated by neurologists regarding the nature of aphasia. Certain investigators (Marie, Goldstein) have felt that the symptoms represent a loss in basic aspects of intelligence, whereas others (Hughlings, Jackson, Head, Weisenburg and McBride, Kennedy and Wolf) have concluded that aphasia per se represents only an impediment in the avenues for expression and reception. Should this latter interpretation be correct, a conclusion that the Wechsler-Bellevue is not a legitimate measure of intelligence for dysphasic *S*s would be supported.

The difficulties encountered on the performance subtests by the group with right cerebral lesions may be similarly viewed. If the results reflect only or primarily a loss in modality functions, the value of the test for estimating intelligence in patients with focal brain lesions is open to question.

SUMMARY

The Wechsler-Bellevue Scale (Form I) was administered to 14 patients with lesions in the left hemisphere of the brain, 17 patients with right-sided cerebral lesions, and 31 patients with diffuse lesions involving both hemispheres. The lesions were localized only on the basis of clinical neurologic and neurosurgical evidence, and the possibility of unknown bilateral involvement was present. The *S*s were not individually matched between groups because of the relative unavailability of patients who met our criteria for unilateral lesions. Nevertheless, the groups were similar with regard to age and formal education. All patients were right-handed.

Thirteen of the 14 patients with left-sided lesions had lower verbal than performance total weighted scores. Fifteen of the 17 patients with right-sided lesions, however, had a higher verbal than performance total. The patients with diffuse lesions were approximately evenly distributed with respect to higher verbal or performance averages. The mean verbal subtest scores for the right-sided group were higher in every instance than for the left-sided group. On the performance subtests this situation was reversed, the left-sided group having the higher means in each instance. The mean verbal and performance scores for the group with diffuse involvement showed scarcely any difference. Questions concerning the meaning of these results with respect to intelligence were commented upon.

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EFFECT OF UNILATERAL BRAIN INJURY IN MAN ON LEARNING OF A TACTUAL DISCRIMINATION[1]

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In analyzing effects of brain injury in man, many investigators have looked for losses in previously developed habits and abilities; few have been concerned with effects of such injury on the acquisition of specific habits. The present study describes learning in a group with unilateral brain damage and in a comparable group without brain injury. The task was a somesthetic discrimination in which the discriminanda were presented to the hands several times. If *S* improved, we could say that a perceptual type of learning (3) had occurred.

The particular conditions of the experiment allowed for a unique comparison. The brain-injured group consisted of men with unilateral lesions. Further, tactual discrimination was required of each hand separately. Since it is generally assumed that tactual impulses from one hand are projected predominantly to the opposite hemisphere, we could compare, in the same man, the course of events in the hand projecting primarily to an injured hemisphere with the course of events in the hand projecting primarily to an intact hemisphere. More specifically, we asked whether learning would be impaired with the hand opposite the brain injury.

METHOD

Subjects

The *S*s were drawn from the case file of the Psychophysiological Laboratory of New York University College of Medicine. The population consists of over 300 veterans, primarily of World War II, who sustained penetrating injury to the brain or peripheral nerves. The brain-injured group consisted of 36 *S*s with unilateral loss of cerebral tissue. Eighteen men had lesions of the right hemisphere, viz., 4 frontal, 2 fronto-parietal, 2 fronto-temporal, 1 fronto-temporo-parietal, 2 parietal, 2 parieto-occipital, 1 parieto-temporal, 1 temporal, 1 temporo-occipital, 2 occipital. Eighteen men had lesions of the left hemisphere, viz., 4 frontal, 1 fronto-parietal, 1 fronto-temporal, 4 parietal, 2 parieto-occipital, 1 parieto-temporo-occipital, 3 temporal, 2 occipital. The 36 brain-injured *S*s were tested as they appeared for a series of studies at the laboratory. The only *S*s excluded were those with such severe motor or somesthetic impairment that it was not possible to administer the test in the usual way. The control group consisted of 19 *S*s with injury to peripheral nerves of the leg.

Procedure

The discriminanda were six patterns similar to those used by Franz and his co-workers in studies of tactile transfer (1). The patterns shown in Figure 1 were formed by 1-mm.–thick metal strips projecting 5 mm. above a block. Each block was 42 mm. on a side and weighed approximately 495 gm.

The patterns were concealed from *S*'s view by a box, which has been described in an earlier publication (5, p. 225). The hand to be tested was placed inside the box, palm upward, and the sample pattern was placed on the palm for approximately 5 sec. With the same hand used in feeling the sample, *S* then examined the six comparison objects with either palm or fingertips, and selected the pattern that seemed to him to be identical to the sample. The order of presentation of the sample patterns was the same for all *S*s; the comparison patterns were placed in a random order for each *S*.

The first trial consisted of presentation of the six patterns to the hand ipsilateral to the lesion. The next trial consisted of presentation of the six patterns, in a different order, to the hand contralateral to the lesion. For the remaining trials, the hands were tested in the following order: contralateral, ipsilateral, ipsilateral, contralateral. In the control group, the right hand was arbitrarily designated as the ipsilateral hand, and the left hand as the contralateral hand. Thus there were six trials in all, three to each hand, and for each trial the patterns were presented in a different sequence. For all *S*s, then, the number of correct choices was obtained for the first, second, and third trials with the ipsilateral hand, and the first, second, and third trials with the contralateral hand.

RESULTS

Figure 2 shows the number of correct choices for each hand in brain-injured and control *S*s. (The amount of improvement occurring with repetition is discussed here; the absolute level of performance has been considered elsewhere [2].) In the control group, the score on the

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[1] The program of research of which this study is a part is supported by the Commonwealth Fund of New York, and by the Office of the Surgeon General (Department of the Army), Contract DA-49-007-MD-312.

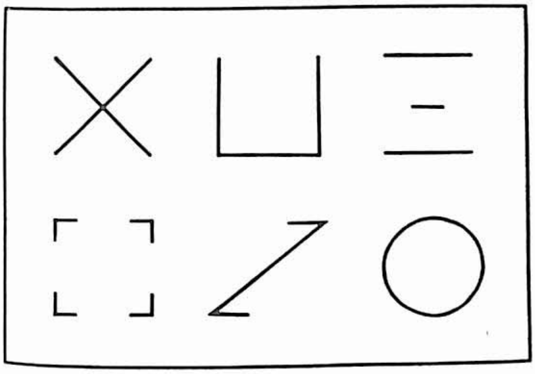

FIG. 1. Tactual patterns. The size of the patterns used was slightly more than twice the size shown here.

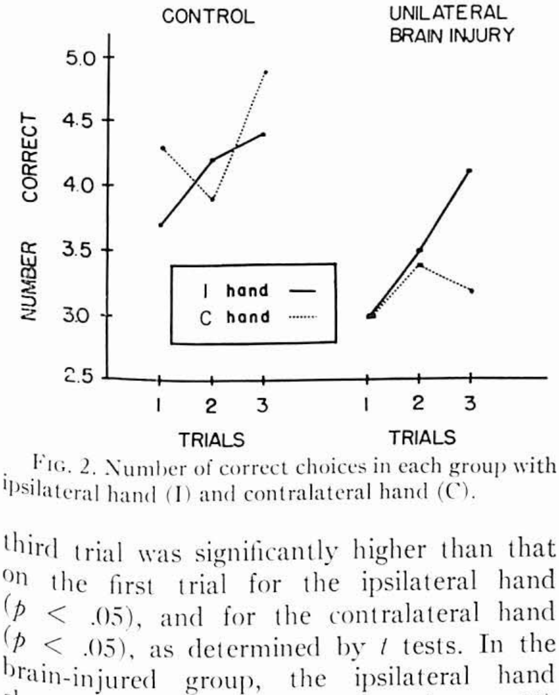

FIG. 2. Number of correct choices in each group with ipsilateral hand (I) and contralateral hand (C).

third trial was significantly higher than that on the first trial for the ipsilateral hand ($p < .05$), and for the contralateral hand ($p < .05$), as determined by t tests. In the brain-injured group, the ipsilateral hand showed significant improvement ($p < .01$) comparable to that of the control group. However, the hand opposite the brain injury did not show significant improvement. Thus, even though the two hands of the brain-injured group showed the same score on the first trial, the curves diverged—one hand improved, the other did not. Significant improvement occurred within a hand, except for the contralateral hand of the brain-injured group.

The next question was whether there was a significant difference between the hands within each group. The amount of change for each hand was calculated by subtracting the score on the first trial from the score on the third trial. In the control group, the mean improvement was 0.7 for the ipsilateral hand, and 0.6 for the contralateral hand; the difference between these means was not significant. In the brain-injured group, the mean improvement was 1.1 for the ipsilateral hand and 0.2 for the contralateral hand; a t test showed the difference between these means to be significant ($p < .02$). Thus the comparison between the hands was consistent with the analysis within the hand—the amounts of improvement for the two hands were the same in the control group but different in the brain-injured group.

Finally, we asked whether there was a significant difference between the groups for each hand. Since the initial level was different for the brain-injured and control groups, analysis of covariance was used. Thus, the scores on the third trial were compared after a correction had been made for the difference in scores on the first trial. If the amount of improvement were the same in each group, the scores on the third trial would not be significantly different from each other. Separate analyses were done for each hand. In the analysis of covariance for the ipsilateral hand, the groups did not differ from each other ($F = 0.20$). In the analysis of covariance for the contralateral hand, however, the groups did differ significantly from each other ($F = 6.21$, $p < .05$).

Since only the contralateral hand failed to improve, the next question was whether this impairment was related to defect in sensorimotor functions. The brain-injured group was divided into those with sign of somesthetic or motor defect of the hands, and those without such signs. The presence of defect was determined by tests of passive movement, touch thresholds, two-point discrimination, point localization, and strength. Sixteen *S*s were free of defect on all these measures, 15 *S*s showed sensory defect alone, 2 showed motor defect alone, and 3 showed both sensory and motor defects. (The small number of men showing signs of both motor and sensory defect may reflect the initial bias in selection, since the procedure was applicable only to those with mild sensory or motor defect.) The results for the sensorimotor and nonsensorimotor groups can be seen in Table 1. It is clear that the contralateral hand did not show improvement

TABLE 1

Number of Correct Choices Made by Each Subgroup, With Comparisons of Differences Between Scores on First and Third Trials

		Contralateral Hand						Ipsilateral Hand					
		Trial			Comparison: Trials 1 and 3			Trial			Comparison: Trials 1 and 3		
Group	N	1	2	3	M_D	S_D	t	1	2	3	M_D	S_D	t
Control	19	4.3	3.9	4.9	.6	.268	2.12*	3.7	4.2	4.4	.7	.332	2.23*
Sensorimotor	20	2.5	3.0	2.8	.3	.291	1.03	2.7	3.4	3.8	1.1	.376	2.92‡
Nonsensorimotor	16	3.6	3.8	3.7	.1	.293	.34	3.3	3.6	4.4	1.1	.269	4.08§
Aphasia	11	2.6	3.0	2.9	.3	.407	.66	2.7	3.9	4.0	1.3	.407	3.12†
Nonaphasia	25	3.1	3.5	3.3	.2	.258	.77	3.1	3.3	4.1	1.0	.308	3.28‡
Epilepsy	10	2.9	3.2	2.9	0	—	—	2.2	3.7	3.4	1.2	.611	1.96
Nonepilepsy	26	3.0	3.4	3.3	.3	.247	1.26	3.3	3.4	4.4	1.1	.252	4.28§
Frontal	15	2.9	3.4	3.0	.1	.336	.39	3.2	3.2	3.9	.7	.396	1.84
Nonfrontal	21	3.1	3.4	3.3	.2	.286	.98	2.8	3.7	4.2	1.4	.305	4.53§
Parietal	16	2.9	3.4	2.8	−.1	.347	.20	3.1	3.5	4.2	1.1	.379	3.14‡
Nonparietal	20	3.1	3.4	3.5	.4	.266	1.69	2.9	3.5	4.0	1.1	.328	3.20‡
Temporal	10	3.3	3.7	3.5	.2	.467	.43	3.0	3.5	4.6	1.6	.400	4.00§
Nontemporal	26	2.8	3.3	3.1	.2	.240	.96	3.0	3.5	3.9	.9	.298	3.05‡
Occipital	10	3.3	3.5	3.8	.5	.373	1.34	3.1	3.7	4.1	1.0	.447	2.24
Nonoccipital	26	2.8	3.4	3.0	.2	.260	.77	2.9	3.4	4.1	1.2	.297	3.90§
Left hemisphere	18	2.9	3.0	3.2	.3	.266	1.05	2.7	3.6	3.8	1.1	.392	2.71†
Right hemisphere	18	3.1	3.8	3.2	.1	.345	.46	3.2	3.4	4.4	1.2	.305	3.83‡

* $p < .05$; † $p < .02$; ‡ $p < .01$; § $p < .001$.

Note.—The pairs of defect and lesion groups were formed by dividing the brain-injured *Ss* into two groups, those with the characteristic under consideration, and those without it. For example, the sensorimotor group consisted of the brain-injured *Ss* with sensorimotor defect, and the nonsensorimotor group consisted of the brain-injured *Ss* without sensorimotor defect. The other groupings were formed in the same way, considering each characteristic independently.

in either group. The ipsilateral hand, however, showed significant improvement in both groups. It is noteworthy that the ability of the nonsensorimotor group to discriminate the patterns on the first trial (with either hand) was only slightly below that of the control group.

Since the impairment was not related to sensorimotor defect, other variables were investigated: locus of lesion and presence or absence of aphasia and of epilepsy. (The methods for determining locus, and for subdividing the group, have been previously described [5].) Regardless of the way in which the group was divided, the contralateral hand never showed a significant improvement (Table 1). The ipsilateral hand always showed consistent improvement, which reached a significant level in all but three subdivisions, the frontal, occipital, and epilepsy groups. In these three groups, the *t* values fell between the .10 and .05 levels; none of the *t* values for the contralateral hand ever reached the .10 level of probability. Since the frontal, occipital, and epilepsy groups never differed from their complementary subgroups, it is likely that the improvement shown by the former groups represents a real change that would reach a significant level with a larger number of *Ss* in each group.

DISCUSSION

The impairment of the brain-injured group appears to be dissociable from defect in primary functions, and dissociable from general deterioration. That is, lack of improvement in tactual discrimination was unrelated to sensorimotor defect of the hands. Nor could the impairment be due to loss of intelligence, since the same *S* showed improvement with one hand but not with the other. The impairment can best be described as a difficulty in learning, if learning is considered to be improvement in discrimination performance that appears with repeated trials.

Surprisingly, the learning impairment was confined to the hand opposite the injured hemisphere. The finding that an impairment in learning can appear unilaterally speaks against equipotentiality (4) of the two hemispheres for all learning. Equipotentiality would require that learning be impaired with both hands, or with neither hand. However, since a lesion anywhere in the hemisphere may produce the learning defect, our data are consistent with the possibility of equipotentiality within one hemisphere.

Learning was studied under rather special conditions in this experiment. (The data were originally gathered, not for an investigation of learning, but as part of a larger study of tactile discrimination.) The task was more in the nature of perceptual learning (3) than stimulus-response learning. The *S* knew that the correct response was to match the standard and comparison patterns. Further, the various choices were not selectively reinforced since *S* was not informed of the correctness of his response. Difficulty in learning may have been enhanced by the procedure of changing from hand to hand during testing. We do not know how the impairment in learning is related to the specific conditions described here. Further, we do not know whether a normal amount of learning would occur with the hand contralateral to the injury if a greater number of trials were given.

Regardless of these strictures, our results pose two problems concerning the relation of the brain to learning. First, it is necessary to conceive of learning as a process that can, at least under some circumstances, be disturbed unilaterally. Second, one must consider how brain injury at maturity can interfere with some learning processes, perhaps without necessarily impairing the initial level of discriminatory ability.

SUMMARY

This study was concerned with the effect of unilateral brain injury on learning of a tactile pattern discrimination. The experimental group consisted of 36 *S*s with unilateral, penetrating brain injury; the control group consisted of 19 *S*s with leg injuries.

In the control group, significant and equal amounts of improvement occurred with each hand. In the brain-injured group, the hand on the same side as the injury showed significant improvement, comparable to that of the control group. The hand opposite the lesion, however, did not show significant improvement. This lack of improvement was not related to sensory defect, nor was it related to the lobe injured.

Thus, an impairment in learning appeared after unilateral brain injury, but this impairment was confined to the side opposite the lesion. These data emphasize the importance, for some learning, of that hemisphere which receives the main projections from the stimulated surface.

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AN EFFECT OF ELECTROCONVULSIVE SHOCK ON A CONDITIONED AVOIDANCE RESPONSE[1]

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Several authors, notably Mowrer (11) and Miller (10), have suggested that a conditioned avoidance response (CAR) involves a dual stimulus-response sequence in which an internal state of fear becomes conditioned to an external stimulus event, and the avoidance response becomes conditioned to internal stimuli associated with this conditioned fear. According to this view, the conditioned fear has drive properties, and the reduction of fear is considered to be the reinforcing agent which maintains the CAR. If this view is correct, any procedure which attenuates the internal state of fear should attenuate correspondingly a CAR mediated by fear.

Hunt and Brady (8) have shown that a conditioned emotional response (CER) can be markedly attenuated by a series of electroconvulsive shock (ECS) treatments. The CER consists of crouching, defecating, and cessation of instrumental lever-pressing for a water reward at the onset of a previously neutral stimulus which has been paired with a painful shock. Insofar as the CER reflects an internal fear state, this experiment might be interpreted as evidence for the attenuation of fear by ECS (3). This would suggest that a CAR, insofar as it is mediated by fear, should also be attenuated by ECS. This prediction is given some confirmation in a report by Masserman and Jacques (9), who found that ECS tends to eliminate experimental neurosis, which included large avoidance components, in cats.

On the other hand, Gellhorn (4, ch. 15) has reviewed a series of experiments, conducted by himself and his collaborators, which indicated a fully established CAR is not affected by ECS or insulin coma, while a CAR which has been "inhibited" (i.e., extinguished) by nonreinforcement is reinstated by either of these procedures. He further reports that a weak CAR is made stronger by treatment with insulin coma. The reinstatement of extinguished CAR's by ECS has also been reported by Hamilton and Patton (6); however, they report that this effect is of short duration.

The available data indicate that the attenuation of a CER by ECS depends upon the intensity of the painful shock (UCS) employed in conditioning (5), upon the number of ECS (3, 8), and the intervals between training, treatment, and testing (1, 2). The previous studies of the effect of ECS on a CER, on experimental neurosis, and on a CAR differ markedly in these details of experimental procedure. The disagreement among the results may be due, at least in part, to such differences in procedure. The present study was designed to determine the effect of ECS on a CAR when these variables are kept within the limits under which ECS has been shown to have an attenuating effect on a CER.

METHOD

Subjects

In the main experiment reported here, 60 naive, male, albino rats, 50 to 70 days old at the beginning of the experiment, served as *Ss*. Seventeen of these animals either died or were crippled by the ECS procedure; the data from these animals were not included in the analysis of results.

Conditioning Apparatus

The conditioning apparatus consisted of a circular alley having walls 8 in. high of transparent plastic, and a grid floor, 4.25 in. wide, of radially placed brass rods. The outside circumference of the alley was approximately 104 in. The alley was divided into six equal sections by transparent, one-way doors which permitted the *Ss* to move from section to section in a counterclockwise direction only. Each section of the grid floor could be independently charged by an electric current delivering a mildly painful shock (approximately 0.6 ma., 60 cycles, with relatively constant current and voltage). Brief shocks of only 0.05-sec. duration, timed by a synchronous motor and cam arrangement, were delivered every half-second beginning within no more than ½ sec. after the shock key was depressed. A 7.5-w. bulb at the center of the alley permitted a change in illumination to be used as a conditioned stimulus. The entire alley was covered by removable, fine-mesh wire screen to prevent the *Ss* from escaping from the alley.

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Preconditioning and Conditioning Training

During the first 17 days of training (preconditioning) each *S* was placed in the circular alley in a dimly illuminated room for 1.5 min. per day without any presentation of either a conditioned stimulus (CS) or unconditioned stimulus (UCS). A record was kept of the number of sections traversed by each *S*. Prior to conditioning, the *Ss* were divided into an avoidance group ($N = 30$) and a control group ($N = 30$), matched on the basis of the mean number of sections traversed during the last five adaptation trials.

On the first and subsequent conditioning trials, a CS was presented to each *S* after 45 sec. in the alley. This CS consisted of a decrease in illumination accomplished by turning off the 7.5-w. light in the center of the alley for 2 sec. For the *avoidance group* the CS was terminated after 2 sec. If *S* moved to an adjoining section of the alley during this period, no painful shock was administered. However, if *S* failed to move during the 2-sec. CS, the first of a series of 0.05-sec. painful shocks (UCS) was delivered within a half-second after the termination of the CS. Repeated shocks of like duration continued to be given at half-second intervals until *S* entered the adjoining section. To avoid punishment of a correct avoidance response, the shocks were ordinarily terminated as soon as *S* began going through the door, but they were resumed immediately if *S* stopped short of a complete movement to an adjoining section. Each *S* was returned to its home cage after 1.5 min. in the alley.

For the *control group*, the CS (decreased illumination) was applied for 2 sec., as for the avoidance animals, but no UCS (painful shock) was given. Otherwise, treatment for the two groups was identical. The data from the control group were used as a measure of the *Ss*' unconditioned reaction to the CS before and after ECS.

The necessity for such a control was clearly illustrated in a preliminary experiment in which a CS (turning on a 40-w. light) was terminated as soon as the *Ss* moved to an adjoining section of the alley. Under these conditions, control animals rapidly developed an escape reaction to the CS after ECS, even though the CS had never been paired with painful shock. Animals that were not given ECS failed to develop such an escape reaction to the CS. Apparently, the CS was made more aversive by ECS treatment. Since both a CAR and an escape reaction to an aversive CS would appear as movement to an adjoining section of the alley, at the onset of the CS, it was not possible to measure independently these two responses or to determine accurately the effect of ECS on a CAR. By making the duration of the CS independent of *S*'s behavior in the present experiment, the possibility of such an artifact was greatly reduced.

Movement to an adjoining section of the alley during the 2-sec. duration of the CS was arbitrarily defined as a "correct" response. Since each animal ordinarily moved from section to section at a fairly consistent rate during the entire period in the alley, some of these movements would occur during the CS by chance. The probability of such movements during the CS increased as a function of the avoidance training, but some of the correct responses could still be attributable to the general level of activity in the alley. The number of sections traversed during the first 45 sec. in the alley (prior to the CS) was recorded as an index of general activity to permit a correction for activity and for the effect of ECS on activity.

The animals received one conditioning trial per day for 59 days. At this point, 60 per cent of the avoidance *Ss* responded correctly to presentation of the CS. With pretreatment strength of the CAR at this level, either an increase or a decrease in the strength of the avoidance response easily could appear after ECS. Prior to treatment the control group and the avoidance group were each divided into ECS ($N = 18$) and pseudo-ECS ($N = 12$) subgroups, matched on the basis of both the mean number of correct responses and the mean number of sections traversed prior to the introduction of the CS (i.e., activity) during the last five conditioning trials.

Treatment Apparatus and Procedure

The ECS apparatus (8) delivered approximately 35 ma., 60 cycles, with relatively constant current and voltage, through moistened electrodes clipped to *S*'s ears. The duration of stimulation was approximately 0.2 sec. for the first four treatments and approximately 0.4 sec. for the last ten treatments. Full grand mal convulsions occurred in all animals except those crippled by the treatment procedure, and the data from these animals were not included in the analysis of results or in the figures. Exclusion of the data from the animals killed or crippled by ECS did not materially alter the pretreatment matching of groups with respect to either general activity or number of correct responses. Beginning 24 hr. after the last conditioning trial, ECS animals received two convulsive treatments per day for seven days. Pseudo-ECS animals received equivalent handling and had the electrodes clipped to their ears, but no current was used.

Posttreatment Retention Tests

Retention tests were begun on the fourth day after the last ECS treatment and were given, one each day, for ten successive days. The CS was presented as usual during these ten trials, but without reinforcement by the UCS.

RESULTS

Figure 1 illustrates the sharp decline in number of correct responses after treatment

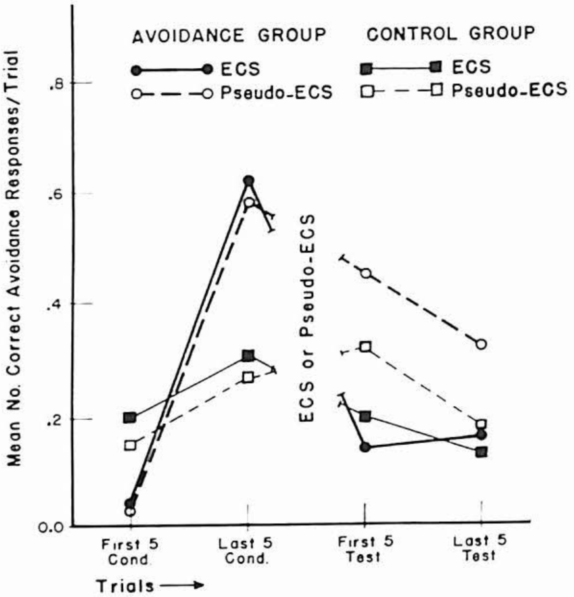

FIG. 1. The effect of training and treatment procedures on a conditioned avoidance response.

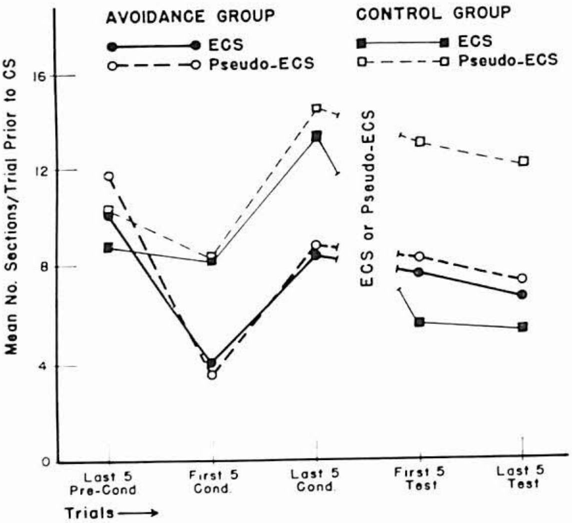

FIG. 2. The effect of training and treatment procedures on general activity.

among convulsed *S*s as compared with nonconvulsed *S*s in the avoidance group. A smaller reduction in number of correct responses also appears after ECS in the control group.

Since correct responses were defined in terms of activity (movement from section to section) during a specific segment of the total running time, a change in *general* activity due to ECS might result in an apparent change in the strength of the CAR. A certain proportion of the total number of movements from section to section would be expected to occur, by chance, during the CS. Figure 2 illustrates the sharp decline in general activity after ECS among convulsed *S*s in the control group only. No appreciable reduction in general activity was observed among convulsed *S*s in the avoidance group. The mean number of sections traversed during the first 45 sec. in the alley (prior to the CS) was used as an index of general activity. No CS or UCS was ever presented during this period; therefore, this measure of general activity would not be confounded by the occurrence or nonoccurrence of correct avoidance responses.

Factors which were not related to the difference in treatment procedure (e.g., temperature variations from day to day) might have resulted in a change in activity between the conditioning and test trials. However, any change due to ECS should appear only among the convulsed *S*s. Therefore the median percentage of change in activity between the last five conditioning trials and the first five post-treatment test trials was determined for the entire control group (ECS plus pseudo-ECS) and, similarly, for the entire avoidance group. Only those *S*s that showed a greater loss in activity than the median loss for their respective groups were scored as showing reduced activity due to the treatment procedure. For example, the median loss in activity for the entire control group was 23 per cent. Animal no. 1 (ECS-Control) traversed 28 per cent fewer sections prior to the CS on the first five test trials than on the last five conditioning trials. This was a greater loss in activity than the median loss for the entire control group; therefore animal no. 1 was scored as showing a loss in general activity due to ECS.

Chi squares, corrected for discontinuity, were computed for the control group and for the avoidance group to determine whether more ECS or more pseudo-ECS animals showed a loss in activity which could be attributed to differences in the treatment procedure. An equivalent analysis was made in terms of percentage of change in number of correct avoidance responses, using the median percentage of change in each group as the cutting point, to determine whether more ECS animals or more pseudo-ECS animals showed a loss in the number of correct responses which could be attributed to differences in treatment.

TABLE 1

The Number of Animals Showing a Loss or Failing to Show a Loss in General Activity and in the Number of Correct Responses Due to Differences in Treatment Procedure

Group	Mdn. % Change	Treatment	Number of Animals		Chi square[*]
			No loss	Loss	
General Activity					
Contr.	−23	ECS	1	8	8.05[†]
		Pseudo	10	2	
Avoid.	+1	ECS	4	6	0.18
		Pseudo	7	5	
Correct responses					
Contr.	0	ECS	5	4	0.8
		Pseudo	10	2	
Avoid.	−55	ECS	1	9	8.98[†]
		Pseudo	10	2	

[*] All chi squares corrected for discontinuity.

[†] Significant beyond the .01 level of confidence.

Table 1 summarizes the effect of ECS on general activity and on the number of correct avoidance responses. Activity was significantly reduced among convulsed *S*s in the control group but not in the avoidance group. Conversely, the number of correct avoidance responses was significantly reduced among convulsed *S*s in the avoidance group but not in the control group.

If ECS had altered the unconditioned running response to the CS, the convulsed *S*s in the control group would have shown either an increase or a decrease in running behavior during the CS (correct responses) as compared with their running during non-CS periods (activity). Three ECS animals and five pseudo-ECS animals in this group showed a greater percentage of loss in correct responses than in activity, while six ECS animals and seven pseudo-ECS animals showed a smaller percentage of loss in correct responses than in activity. Since this difference does not approach significance (chi square less than 0.01), ECS apparently did not alter the unconditioned running response to the change in illumination which was used as a CS for the avoidance group.

Since ECS did not affect activity in the avoidance group, the difference in number of correct responses between ECS and pseudo-ECS animals in this group cannot be attributed to the effect of ECS on general activity. Furthermore, there is no indication that the unconditioned response to the CS was altered by ECS in this experiment. Therefore,the difference in number of correct responses between ECS and pseudo-ECS animals in the avoidance group indicates that ECS attenuated the conditioned avoidance response quite apart from these possible artifacts which are not related to the avoidance-conditioning procedure.

The observed reduction in general activity after ECS among control animals is not surprising in view of previous reports (12) that general activity is depressed by ECS. In the avoidance group activity had already been depressed, presumably by the conditioning procedure (see Fig. 2), and no further reduction in activity was occasioned by ECS.

DISCUSSION

If the assumption is made that a CAR is mediated by fear, the data presented here are superficially consistent with the hypothesis that ECS attenuated the CAR through a reduction in fear. However, the convulsed animals in the present study regularly showed exaggerated startle responses, persistent struggling to escape, and greatly increased attack behavior toward each other and toward *E*. A similar increase in apparent emotionality has been reported by other investigators (3, 7). Such behavior does not seem to be consistent with a statement that fear was reduced by ECS.

Increased emotionality is indicative of increased drive. The apparent increase in drive after ECS might well account for an increase in the strength of conditioned responses. Gellhorn (4, ch. 15) has attempted to account for an increase in the strength of weak CAR's and the reinstatement of extinguished CAR's in terms of increased general excitation associated with heightened sympathetico-adrenal activity and hypothalamico-cortical discharges resulting from ECS and related procedures. In Pavlovian theory, this general excitation assumes many of the functions assigned to drive in more recent theories of behavior. The importance of this mechanism cannot be denied or ignored, but increased general excitation cannot account for both the increase in the strength of a CAR reported by Gellhorn and the attenuation of a CAR observed in the present study.

Mowrer (11) and Miller (10) assume that fear has both drive properties and stimulus properties. According to this view, the stimulus properties of fear constitute the CS which elicits a CAR. Fear stimuli are presumed to be response-produced stimuli; therefore a change in the internal fear response would result in a changed (different) internal fear stimulus. The measurement of internal fear responses has been concerned primarily with physiological changes which are mediated, at least in part, by the hypothalamus and autonomic nervous system. Therefore, the activity of the hypothalamus and the magnitude and balance of autonomic nervous system activity have proved to be useful indices of fear. Gellhorn (4, ch. 18) has reported marked changes in the activity and reactivity of the hypothalamus and autonomic nervous system after ECS and related procedures If this is the case, response-produced stimuli under the control of these structures are changed or distorted by ECS so that they are no longer the same stimuli and cannot be expected to elicit the same responses.

If this general line of thinking is correct, ECS would be expected to exert two opposing effects on responses to fear. Distortion of the response-produced stimuli would be expected to attenuate fear-mediated responses along a gradient of stimulus equivalence. On the other hand, increased drive would be expected to increase the strength of all conditioned responses along this gradient. The balance between these two opposing effects of ECS would depend upon the details of experimental procedure and might determine the direction and magnitude of the effect of ECS on fear-mediated responses.

The present study differs from other studies of the effect of ECS on a CAR in several details of conditioning procedure, the amount of ECS, and the interval between treatment and testing. Previous research (1, 2, 3, 5, 8) has shown that these variables are important in determining the effect of ECS on a CER, and they may be equally important in determining the effect of ECS on a CAR. The details of conditioning procedure would determine the amount of stimulus generalization and, thereby, the amount of attenuation which would result from a given amount of change in the fear stimulus. The amount of ECS would determine the extent of change in the fear stimulus. Hamilton and Patton (7) report that reinstatement of an extinguished CAR is transitory and cannot be demonstrated 48 hr. after the last ECS. Therefore, the period between treatment and testing appears to be of great importance.

SUMMARY

Sixty male albino rats served as *S*s in this experiment. They were divided into an avoidance group ($N = 30$) and a control group ($n = 30$), matched on the basis of their locomotor activity in a circular alley prior to conditioning. The avoidance animals were given 59 conditioning trials, one per day, during which they learned to avoid a .6-ma. painful shock by moving forward to an adjoining section of the alley at the onset of a CS (reduced illumination). The control animals were given equivalent training in the alley, except that the CS was never reinforced by painful shock. Eighteen of the 30 animals in each group were then given 14 electroconvulsive shock (ECS) treatments. Retention tests were begun on the fourth day after the last ECS treatment to determine the effect of ECS on general activity and on the retention of the conditioned avoidance response.

The general level of activity in the alley was significantly depressed by ECS in the control animals but was not affected by ECS among animals that had received avoidance conditioning prior to treatment.

The conditioned avoidance response was significantly attenuated by ECS. Changes in general activity and changes in the unconditioned response to the CS were ruled out as determinants of this attenuation.

It was tentatively assumed, for present purposes, that a conditioned avoidance response is mediated by fear. An attempt was made to account for the effect of ECS on such responses to fear in terms of changes in fear stimuli associated with changes in hypothalamic and autonomic activity and in terms of drive changes resulting from ECS. Alternative interpretations were not ruled out.

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A FURTHER STUDY ON THE RETROACTIVE EFFECT OF ECS

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Numerous studies have shown that convulsive shock particularly affects memories of newly acquired habits (cf. 1). Only very recently, however, has an attempt been made to investigate the functional relationship between the degree of memory loss and the age of the acquired habit. In a study by Duncan (2), rats were trained on an avoidance conditioning problem, receiving one trial daily for a total of 18 days. In one group, an ECS was induced 20 sec. after the termination of each trial. Additional groups received one ECS 40 sec., 60 sec., 4 min., 15 min., 1 hr., 4 hr., and 14 hr., respectively, after each trial. Duncan's results showed that if an hour or more elapsed between the end of the trial and the induction of the convulsion, there was no apparent memory loss. If induced within 15 min., however, a significant deficit in memory was observed as shown by the depressed learning rate of the avoidance response. The observed deficit was inversely related to the length of time intervening between the completion of the trial and the onset of the convulsion. Gerard (3) reports a study similar to the one by Duncan in which hamsters were given an ECS at varying intervals after the termination of each trial in a maze situation. The results obtained from this study were essentially the same as Duncan's, except that the administration of an electroshock after 1 hr. still had some retarding effect on maze performance.

It is to be noted that the results derived from these two studies are complicated by at least two factors other than disruption of the memory trace. Since a number of shocks was given to the *S*s during the course of each experiment, the observed retardation in learning may have been aggravated by the cumulative effects of repeated convulsions. In addition, the *S*s that received convulsions very shortly after each trial may have been subject to some negative conditioning to the goal box.

The present study attempted to investigate this functional relationship without the complications inherent in the foregoing experiments. To eliminate the cumulative effects of repeated convulsions and to reduce the possibility of negative conditioning to the goal box, the effect of only one ECS was studied. This necessitated giving a single convulsive shock at varying intervals after the completion of learning.

In a previous paper (10), a discrimination box was described which utilizes the motive of avoidance of shock. With this apparatus, it is possible to train rats by means of massed practice on a visual discrimination (e.g., horizontal vs. vertical stripes) with relative ease. In the present experiment, rats were trained in one session to a criterion of learning after which a single ECS was given at varying intervals subsequent to mastery of the discriminative response. Its effects upon memory were tested two days later.

METHOD

Subjects

Sixty male albino rats of the Harlan strain were used as *S*s. At the beginning of experimental training, the *S*s were from 65 to 100 days of age. All *S*s were kept in individual cages and had continuous access to food and water. Individual handling was practiced four days prior to the beginning of preliminary training.

Apparatus

The discrimination apparatus may be seen in Fig. 1 in a previous paper (10). It consisted of a start box, a V-shaped choice chamber, and a goal box. Between the start box and the choice chamber was a vertical sliding door made of transparent plastic. The floor of the start box and the choice chamber was made into a grid consisting of transversely placed bronze rods, $\frac{3}{16}$ in. in diameter. The goal box had a floor made of wood. Two windows, $3\frac{1}{2}$ in. square, appeared at the end of the choice chamber. They provided the only means by which *S* could enter the goal box. Midway between the windows was a vertical partition which extended 3 in. into the choice chamber. The entire apparatus was illuminated by one 100-w. bulb placed 4 ft. directly above the choice chamber and two 75-w. bulbs mounted just behind the start box.

A separation of $\frac{1}{2}$ in. existed between the bronze rods, save for the area extending from the base of each window to the end of the vertical partition. Here, the rods were separated by only $\frac{1}{4}$ in. The grid sections extending 3 in. in front of each window were so wired that either the left or the right section could be charged by manipulation of a knife-switch. All parts of the grid were connected to an a.c. source of 35 v.

The cerebral shock apparatus was the same as that described by Hayes (4), except that the 0.5-sec. duration of the current was regulated by a Hunter timer, mod. 1110-B. A current strength of 50 ma. was delivered by means of alligator clips mounted on *S*'s ears.

Procedure

Preliminary training. On Day 1, each *S* was trained to run from the start box into the goal box in order to avoid shock. The *S* was first placed in the start box, and the door was raised. If *S* failed to leave the start box within 5 sec., the grid current was turned on briefly. Failure to enter the goal box within 30 sec. was followed by another brief shock. Training was continued until *S* successfully ran from the start box into the goal box ten times in succession without the aid of shock.

On Day 2, medium gray cards were placed against the windows through which *S* was trained to run. In order to familiarize *S* equally with both windows, one card was locked. The locked card was rotated at random from the left to the right window.

On Days 3, 4 and 5, all *S*s were trained on a brightness discrimination involving homogeneous gray cards differing only in reflectance. The light card constituted the positive stimulus. A response to the positive card admitted *S* to the goal box. The negative card, on the other hand, was locked. Punishment for errors was given by charging the grid under which the negative card was located. The method of correction was necessarily used. The positive card was switched from the right to the left window in a prearranged random order. The specific training procedure was as follows: *S* was placed in the start box, and the door was raised. If *S* failed to leave the start box within 5 sec., a shock was delivered through the grid. No further shock was given unless *S* committed an error. An error was defined as an approach response to the negative card which brought *S*'s forefeet in contact with the "hot" grid. (Although the intensity of the shock was relatively weak, traversal of the energized grid by *S* was readily observed). Twenty-five trials were given each day with an intertrial interval of 45 sec.

Test problem. On Day 6, all *S*s were trained on the horizontal-vertical discrimination. The *S*s were first divided into five groups of 12 *S*s each, matched on the basis of performance on the last two days on the brightness discrimination.

Each group was given massed training on the horizontal-vertical problem until the criterion of nine correct responses out of a series of ten trials was reached. At varying intervals after meeting the criterion, one ECS was given. For one group, an electroshock was administered 10 sec. after the last criterion trial was completed. For three additional groups, an electroshock was given 2 min., 1 hr., and 4 hr., respectively, after completing the last criterion trial. Grand mal convulsions were evoked in all experimental *S*s. The fifth group constituted the normal controls to which no ECS was administered.

The stimulus cards consisted of alternating black and white stripes, the thickness of the striations being ½ in. Half the *S*s within each group were trained positively to vertical stripes, the other half to horizontal stripes. The specific training procedure employed throughout original learning was the same as that used in the brightness discrimination during preliminary training.

Following a rest period of two days, all groups were required to relearn the same discrimination. The conditions of training were identical to those involved in the original learning. Training on Day 8 was continued until the criterion of nine correct responses out of ten trials was reached.

RESULTS

Table 1 presents the original learning data for the five groups on the horizontal-vertical discrimination problem. An analysis of variance was applied to each of the performance measures in order to determine if there were any significant differences in initial learning ability among the five groups. The obtained *F*'s for trials to criterion as well as for errors to criterion were less than unity, and obviously not significant.

Since all groups were trained to the same criterion in relearning as in original learning, the savings method was employed to measure the degree of retention. In Figure 1, the mean percentage of savings in trials and in errors are plotted against the time interval (seconds) between the last criterion trial and the onset of the convulsion. It can clearly be seen that the shorter the criterion-shock interval, the greater is the effect of one ECS upon retention. The p values for the differences in percentage savings between the experimental groups and the control group were computed by the use of Wilcoxon's method (11) for unpaired replicates. With respect to both trial and error savings, the control group was significantly superior to the 10-sec., 2-min., and 1-hr. groups (p values were at least at the .02 level of significance). The differences between the 4-hr. group and the control group, however, fell far short of statistical significance. Of particular interest is the performance of the 10-sec. group. The

TABLE 1

Mean Trial and Error Scores to Criterion for Original Learning

Group	Trials	*SD*	Errors	*SD*
10 sec.	17.6	13.60	9.9	7.41
2 min.	17.6	18.63	9.4	11.44
1 hr.	18.9	9.81	8.1	5.47
4 hr.	15.2	10.48	7.3	6.83
Control	17.4	12.65	8.4	9.21

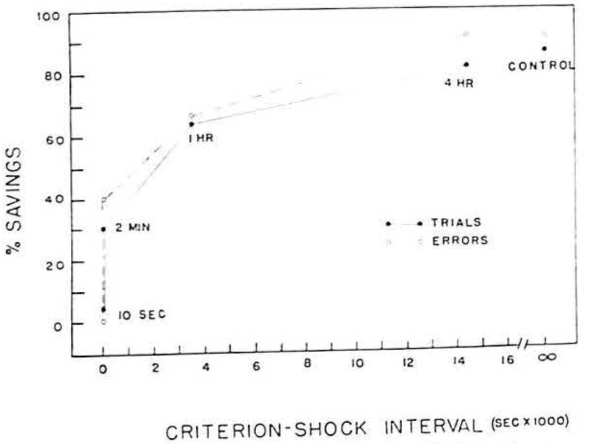

FIG. 1. Mean percentage savings in trials and errors as a function of the length of the criterion-shock interval.

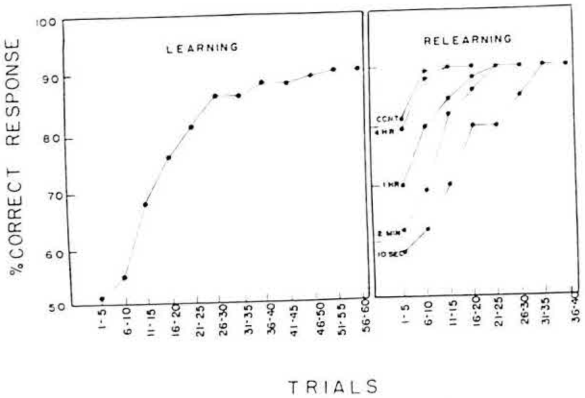

FIG. 2. Performance of the combined groups on original learning and the performance of the separate groups on relearning the horizontal-vertical discrimination problem.

meager percentage savings in trials (4 per cent) and errors (1 per cent) indicate that if a convulsive shock is administered almost immediately after attainment of the criterion, memory of the habit is virtually destroyed.

The performance of the combined groups on original learning and the performance of the separate groups on relearning are summarized in Figure 2. It is to be noted that there is a direct relationship between the length of the criterion-shock interval and the level of performance on the first five relearning trials. The t test revealed that the control group performed at a significantly higher level on the first five trials than either the 10-sec. group ($p = .001$), 2-min. group ($p = .01$), or 1-hr. group ($p = .05$). The difference between the control group and the 4-hr. group again was not significant ($p = .50$).

DISCUSSION

These results are consistent with those obtained by Duncan and Gerard in two main respects: (*a*) there is a certain time lapse after learning beyond which the induction of electroshock has no effect upon memory, and (*b*) within a certain time interval after learning, the deficit in memory is inversely related to the length of time between the completion of training and the onset of the convulsion. For the single-trial method, Duncan found that shock had no effect after an interval of about 15 min., whereas Gerard found shock to be effective after 1 hr. For the complete learning method used in the present experiment, shock was effective in impairing memory after 1 hr., but not after 4 hr. This difference in the temporal effectiveness of ECS may be a function of a number of variables, such as the stage of learning at which shock is given, the degree of distributed practice, the type and difficulty of the learning problem, and the number of electroshocks administered.

The combined results of the foregoing studies strongly support a perseveration theory of memory (9) which holds that the neural activity involved in the learning must persist for some time after the completion of formal training in order to be fixated. During this period of perseveration, the memory trace is presumed to be susceptible to interference. Gerard (3) has suggested that the neural process underlying perseveration may be reverberatory activity. The reverberatory circuit which has been proposed by others (6, 8) to be the model of recent memory would seem to explain the susceptibility of newly acquired habits to convulsive shock. Application of this hypothesis to visual discrimination learning in the rat, however, does not seem likely. On the basis of Lashley's analysis of the rat's visual system (7), it appears that all the cells within the striate cortex are firing under conditions of light adaptation. Since there is good evidence that memory of discriminative habits based on brightness and form are localized within this area in rats, reverberation would have to be sustained for at least 1 hr. in the presence of a continuous influx of impulses resulting from retinal stimulation. Although reverberation may still be a factor, the existence of some additional neural process operating after cessation of learning trials seems necessary. Recent data suggest that neuronal metabolism may be a factor since the administration of anoxia soon after learning has the same retarding effects on memory as does ECS (5).

SUMMARY

Five groups of rats were given training on a horizontal-vertical discrimination problem. For four groups, one electroconvulsive shock was administered at 10 sec., 2 min., 1 hr., and 4 hr., respectively, after reaching the criterion of mastery. The fifth group constituted the normal controls. Two days later, all groups were required to relearn the discrimination.

The results of this study showed the following:

1. The groups receiving a shock at 10 sec., 2 min., and 1 hr. after mastering the discriminative response showed significant deficits in memory of the habit, the deficit being inversely related to the time interval.

2. There was no significant difference in retention of the habit between the control *S*s and those *S*s receiving a shock 4 hr. after learning the problem. These results were discussed in terms of a perseveration theory of memory.

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ANALYSIS OF THE EFFECTS OF FRONTAL LESIONS IN MONKEY: I. VARIATIONS OF DELAYED ALTERNATION[1]

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Delayed alternation and delayed reaction, the two problems consistently failed by monkeys with lesions of lateral frontal granular cortex (3), present the animal with identical alternatives for response. The reward contingencies differ in the two tasks, but in both, the animal is confronted after a delay with two containers which are distinguishable only by their positions—one appearing on the left, the other on the right. The present experiment was undertaken to determine whether or not impairment following frontal damage is related to the "left-right" response choice which these tasks require. To this end, traditional delayed alternation and two *variants* of delayed alternation were presented: In the first variant, frontal operates and controls were trained to displace alternately two cups arranged one above the other; in the second, they were trained to alternate between displacing and not displacing a single centered cup.

METHOD

Subjects

The *S*s were eight immature macaques, all of which had previously undergone one-stage bilateral cortical resections. Four had lesions of anterolateral frontal cortex (LF- 2,- 3,- 5,- 11), three had resections of the inferior convexity of the temporal lobes (IT- 4,- 15,- 25), and one had a ventral frontal ablation (VF-10). The last four animals were used as controls.

Verification of lesions in the four anterolateral frontal operates and in the ventral frontal control, as determined by reconstructions from serial sections, are shown in Figure 1. The anatomical findings for the three inferotemporal controls have been presented elsewhere (2).

The testing experience of these three inferotemporal operates and of the first three anterolateral frontal operates had consisted of pre- and postoperative training on a simultaneous and a successive visual pattern discrimination (2). The two remaining animals (one anterolateral frontal operate and the ventral frontal control) had received preoperative training on the traditional delayed-alternation procedure. The data reported here were obtained in the period between one month and four months after surgery.

Apparatus

Animals were trained in an air-conditioned sound-proofed room. The apparatus consisted of a plywood enclosure divided into two sections: an unlit chamber for the animal cage, and an illuminated section for the testing tray, which was at the level of the cage floor. A sliding panel interposed between the two sections concealed the manipulanda during the delay, and a one-way-vision screen concealed *E* when the sliding panel was raised.

For the traditional "left-right" alternation task (L-R), two containers, 3 in. long, 3 in. wide, and 1 in. deep, were mounted 12 in. apart on the testing tray and were covered by displaceable metal lids. For the "up-down" alternation problem (U-D), two cubicles, 3 in. high, 3 in. wide, and 4 in. deep were set in a square wooden frame, 16 in. on a side, with the upper cubicle 10 in. above the lower. The openings facing the animal were covered by swinging metal doors hinged at the top. For the "go-no-go" alternation (G-N), a single container, of the same dimensions as those used in the L-R task, was mounted in the center of the testing tray and covered by a metal lid.

In all situations, the manipulanda were located a distance of 2 in. from the sliding panel.

Procedure

All eight animals were trained on the three problems in the order L-R, U-D, G-N.

At the start of each daily session, the animal was permitted a free choice in which both cups (the single cup in G-N) were baited. On the next trial (the first scored trial) the correct response was the opposite of that made on the free trial; and on all subsequent trials the correct response was the opposite of that required on the just preceding trial. A daily session consisted of 50 such alternation trials presented by the rerun correction technique; i.e., the reward condition obtaining at the time of an error was left unchanged in subsequent presentations until the animal responded correctly. Each series of such presentations was scored as a single incorrect trial. Since with this method each trial ended with a correct response, animals training on either the L-R or U-D task received 50 peanut rewards daily. On the G-N task, however, they received peanut rewards only for the 25 correct "go" responses; a correct "no go" response (i.e., not displacing the lid) was not rewarded, except in the sense that the subsequent trial became a "go" trial.

All presentations, including the rerun corrections, were separated by 5-sec. intervals. Five seconds was permitted for response.

The animals were trained on a given problem to a criterion of 90 correct in 100 consecutive trials, unless criterion was not attained in 500 trials, at which time

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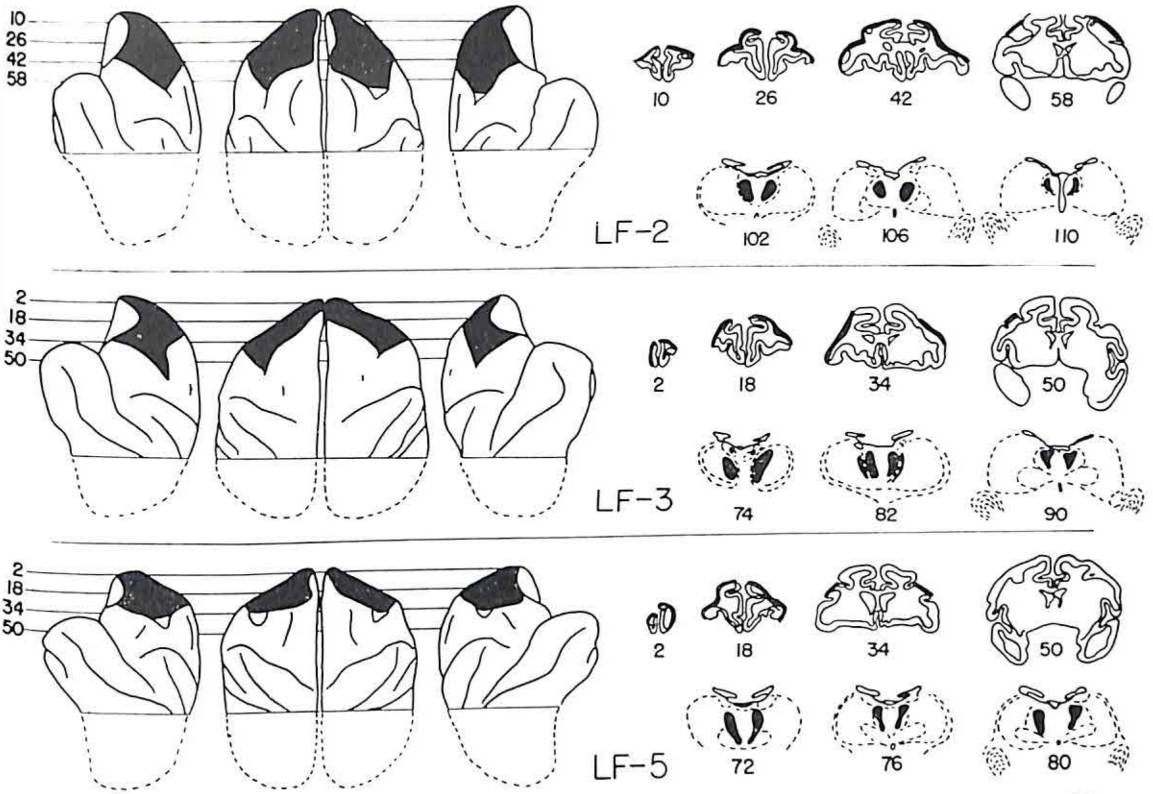

FIG. 1. Lateral and dorsal reconstructions of anterolateral frontal lesions (*LF*) and lateral and ventral reconstructions of ventral frontal control lesion (*VF*). Cross sections through the cerebrum show the depth of the lesions, and sections through the thalami show retrograde degeneration. Black in the reconstructions and cross sections indicates damage; in the thalami black indicates retrograde degeneration.

training on that problem was discontinued and the next problem was presented.

RESULTS

Scores for each task, indicating number of trials received (i.e., excluding corrections), and the correct percentage achieved in the final 100 trials, are given in Table 1.

All control operates (including the animal with the ventral frontal ablations) attained the 90 per cent criterion on all alternation problems in less than the 500-trial limit. In the majority of cases this level was reached in less than 200 trials. In contrast, the anterolateral frontal operates consistently received the max-

TABLE 1
Variations of Delayed Alternation

Subjects	Left-Right (L-R)		Up-Down (U-D)		Go-No-Go (G-N)		Left-Right (L-R)	
	Trials	Per Cent Correct Last 100 Trials	Trials	Per Cent Correct Last 100 Trials	Trials	Per Cent Correct Last 100 Trials	Trials	Per Cent Correct Last 100 Trials
LF-2	500	64	500	52	500	86	500	51
LF-3	500	60	*	*	500	89	500	60
LF-5	500	58	500	53	500	83	500	55
LF-11	500	55	500	59	500	92	500	63
IT-4	100	90	200	90	360	94		
IT-15	100	98	190	91	450	90		
IT-26	110	90	150	91	180	90		
VF-10	160	91	400	90	180	90		

* LF-3 could not be trained to manipulate the swinging doors in the U-D problem.

imum amount of training, and on the L-R and U-D tasks rarely exceeded a score of 60 per cent.

On G-N alternation, however, the final performance of the anterolateral frontal group rose to a remarkably high level. One animal attained criterion; the three others achieved scores above 80 per cent. This superior performance is surprising in view of the fact that the controls generally required more training to learn the G-N task than to learn either of the others.

A breakdown of the corrections into that portion representing extra errors (i.e., excluding the correct response following an error or series of errors) indicated that both anterolateral frontal and control groups required twice as many corrections on G-N alternation as they did on either L-R or U-D. The anterolateral frontal operates, however, averaged nearly 400 extra incorrect responses on the G-N problem; the controls averaged only 50. With rare exceptions the errors of all animals in G-N alternation were made on "no go" trials.

Approximately six months after the animals had completed these three alternation tasks, the anterolateral frontal operates were given 500 additional trials on the L-R problem (see Table 1). In spite of this additional postoperative time and training they failed to show any improvement over their initial performance on this task.

It may be noted that throughout this series of tasks there is no consistent relationship between the scores of the anterolateral frontals and the extent of their lesions as shown in Figure 1.

DISCUSSION

The failure of the anterolateral frontal group on "up-down" alternation demonstrates that the deficit produced by lesions of lateral frontal granular cortex is not related specifically to the "left-right" choice required by traditional delayed-response–type tests. However, the impairment *does* seem to be related to some feature common to the two-cup alternations, since the anterolateral frontal operates performed exceptionally well (final scores averaging 87 per cent) on the single cup "go–no-go" alternation. Factors not directly related to the "go–no-go" response requirements may have contributed to this high level of performance. For example, the anterolateral frontal animals received intensive training on this task due to the large number of corrections they required; in addition, they had received extensive training previously on the two other forms of alternation. It is unlikely, however, that the relatively successful performance of the anterolateral frontal operates on the G-N problem was due exclusively to practice effects, since retesting of "left-right" alternation subsequent to testing on the "go–no-go" procedure did not reveal any improvement on the traditional task. Furthermore, previous results with frontal operates (1, 3) have shown that their scores on classical delayed-response–type tests may remain at a chance level throughout several thousand trials. Their fairly rapid attainment of a high level of performance on the "go-no-go" variation would seem, therefore, to deserve further investigation.

SUMMARY

Four operates with lesions of lateral frontal granular cortex and four operated controls were trained on a series of delayed alternation problems presented in the following order: "left-right" alternation, "up-down" alternation, and "go-no-go" alternation. The control operates required an increasing number of trials to learn the consecutive problems, but all attained criterion on all three tasks. The anterolateral frontal operates, in contrast, failed, within the limits of training, to achieve 90 per cent correct performance on any of the tasks, although their final scores on "go-no-go" alternation fell just short of this criterion. The relatively successful performance of the anterolateral frontal operates on the "go-no-go" procedure cannot be explained entirely as an effect of general delayed-alternation training since comparable improvement did not appear on the classical problem when this task was given subsequently. The results suggest that while difficulty specific to the "left-right" response choice cannot account for frontal operates' severe impairment on traditional delayed-response-type tasks, some factor other than, or in addition to, the delay would appear to be of critical importance.

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LOCOMOTOR REACTION DECREMENT IN NORMAL AND BRAIN-DAMAGED RHESUS MONKEYS[1]

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An initially high or rapidly rising frequency of response often follows the onset of change in an animal's environment. After its early peak, this rate of response decreases to an asymptote in a negatively accelerated manner as a function of time—a phenomenon to be termed "reaction decrement." The specific responses involved may vary. Reaction decrement lately has been demonstrated, for example, by Hinde (5) for the "mobbing" call of the chaffinch in the presence of a predator and by Montgomery (9) for the locomotion of the rat in a maze.

Orderly decremental locomotor reactions are shown by rhesus monkeys placed in a novel environment, a fact which may be used to clarify the nature of locomotion in certain brain-damaged animals. The hypermotility of monkeys with prefrontal lesions has been known at least since the time of Ferrier (2, p. 232), and similar effects of injury to rostral brain loci have been obtained in a wide range of other mammalian species. The present paper reports two experiments to determine for rhesus monkeys (*a*) the normal locomotor reaction decrement pattern following an environmental change, and (*b*) the characteristics of the pattern in animals with extensive damage to either prefrontal or temporal brain tissue. The method of testing was the same throughout.

METHOD

Apparatus

A cubiform activity cage measuring 2 ft. on each edge was constructed with sides made of vertical iron bars with a diameter of $^{3}/_{16}$ in. and spaced 1½ in. apart, center to center. Two cylindrical beams of light, 1½ in. in diameter, were projected through the sides of the cage so as to intersect at its center, 1 ft. above floor level. The beams of unfiltered light were propagated by 30-w. incandescent lamps in Worner, Model 621, light sources. Opposite each light source was a Photobell photorelay unit, Type ES-2, J-2, which produced a 115-v., 60-cycle output whenever the incident light was interrupted by passage of an animal through the beam. Light sources and photorelays were placed at uniform distances of 4 ft. from the sides of the cage. Each relay was connected to the magnet of a second relay located in a nearby room. The second relay translated the output of the photorelay into on-off switching of a pen circuit in an Esterline-Angus recorder, Model AW. A third pen, wired to a switch in the testing room, was used to time the beginning of the experimental session.

No quantitative estimate of contamination of the record by movements of the head and appendages made when a monkey is in a stationary position in the cage is available, but observations made during a pilot study indicate that the index of locomotor activity obtained from beam interruptions consists almost entirely of records of total bodily movement.

The windows of the activity room were covered with opaque paper, and the room illumination was provided by ceiling lamps. During the testing, noises from outside the experimental room were either eliminated or masked with continuous white noise. The interior of the room had not been seen by the *S*s before the experiments.

Procedure

As soon as an animal had been admitted to the activity cage, *E* opened and closed the switch used to time the start of the session and left the room, shutting the door behind him. The *S* remained alone in the experimental room for the duration of the session, 20 min., after which *S* was returned to its home cage. Each test involved multiple testing sessions; and since it was desired to minimize the effects of possible diurnal variation in the level of locomotion, all sessions were given at the same time of day for an individual animal.

EXPERIMENT I

This was undertaken to determine the course of locomotion within and between testing sessions for a group of normal, intact rhesus monkeys.

Subjects and Design

Seventeen normal adolescent rhesus monkeys were used. The primary index of locomotion was the number of beam interruptions made by a monkey in its movements from one quadrant of the cage to another. Data were collected during five testing sessions, each of which was arbitrarily fractionated for purposes of analysis into five, 4-min. periods; individual sessions were given on successive days. Since the results of the pilot study indicated that the distribution of raw scores would show

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[1] These researches were supported in part by the Research Committee of the Graduate School from funds supplied by the Wisconsin Alumni Research Foundation.

a marked positive skewness, each of the scores was transformed by taking its common logarithm after a constant of 1 had been added to eliminate the few zero scores. The design provided for analysis of variance of the data, the main effects being sessions, periods, and animals. The second-order interaction was taken as the estimate of population variance.

Results

The analysis of variance summarized in Table 1 is based upon an approximately normal frequency distribution of transformed scores. The table reveals that when allowances are made for the somewhat different patterns of performance shown by various animals on successive days of testing, the only significant sources of variance in the rate of locomotion are those attributable to differences among animals and to intrasession changes.

Figure 1 shows that under the conditions of this test the rate of locomotion, relatively high at the beginning of the experimental session, declined to an asymptotic level by the fourth 4-min. period. The difference between the initial and final mean rates is of the order of magnitude of 0.5 log unit.

TABLE 1

Summary of Analysis of Variance of Locomotion Scores

Source	*df*	MS	*F*
Sessions (S)	4	0.9615	0.9615/0.0819 = 11.74* 0.9615/0.2046 = 4.70
Periods (P)	4	3.5932	3.5932/0.0819 = 43.87*
Animals (A)	16	3.0244	3.0244/0.0819 = 36.93* 3.0244/0.2046 = 14.78*
S × P	16	0.1978	0.1978/0.0819 = 2.41
S × A	64	0.2046	0.2046/0.0819 = 2.50*
P × A	64	0.0891	0.0891/0.0819 = 1.09
S × P × A	256	0.0819	

* Significant at the .001 level.

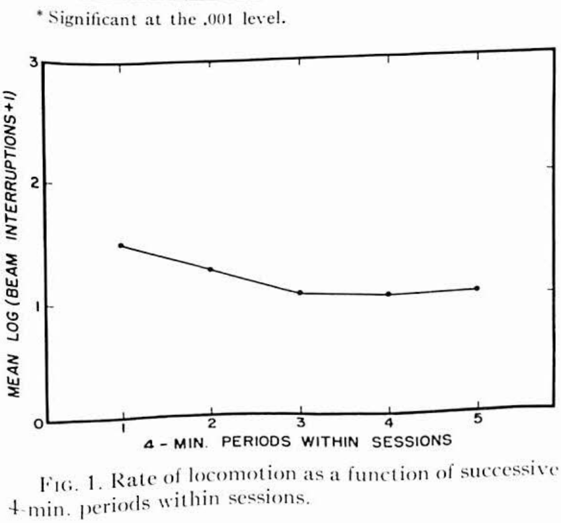

FIG. 1. Rate of locomotion as a function of successive 4-min. periods within sessions.

EXPERIMENT II

This test was designed to compare the overall level, variability, and course of locomotor activity in normal monkeys with those in monkeys with bilateral prefrontal lobectomies and in monkeys with bilateral removal of the neocortex of the temporal lobe.

Of particular interest is the locomotor behavior of the prefrontal monkeys. On an observational basis, Mettler (8) has concluded that the excessive locomotion of monkeys with prefrontal lesions is not an instance of hyperactivity per se, an incremental effect of the lesions independent of environmental events, but of hyperreactivity to external stimuli. Evidence supporting this hypothesis is given by the observation of Kennard, Spencer, and Fountain (6) that prefrontal monkeys are very inactive in the absence of visual stimulation. Additional supportive evidence would be provided if it could be shown that locomotion in prefrontal animals after an environmental change is not only momentarily higher, but also less susceptible to decay, than in normal animals. This would re-emphasize the interaction between physiological state and external stimulation.

Subjects

The 34 monkeys in this experiment, none of which had participated in Experiment I, were assigned to three groups on the basis of anatomical status. Twenty-one unoperated monkeys were used as controls in the normal group. Five animals (no. 129 [53–72], 130 [53–65], 169 [53–81], 171 [53–70], and 172 [53–67]) were in the prefrontal group.[2] In the temporal group, there were 8 monkeys with temporal lobe ablations (no. 147 [53–3], 158 [52–42], 236, 238, 239, 240, 241, and 242). The time of testing varied among the prefrontal animals from the twelfth to the fifteenth postoperative month and among the temporal animals from the sixth to the seventh postoperative month.

Since intergroup comparisons will be made on a statistical basis, and since the lesions of animals in an operated group were grossly similar, only a brief state-

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[2] Two numbers are given for each animal. The first is the number used at the Wisconsin Primate Laboratory. The number in brackets is that used by the Department of Physiology. Both have been included for convenience in making cross references with papers to be published.

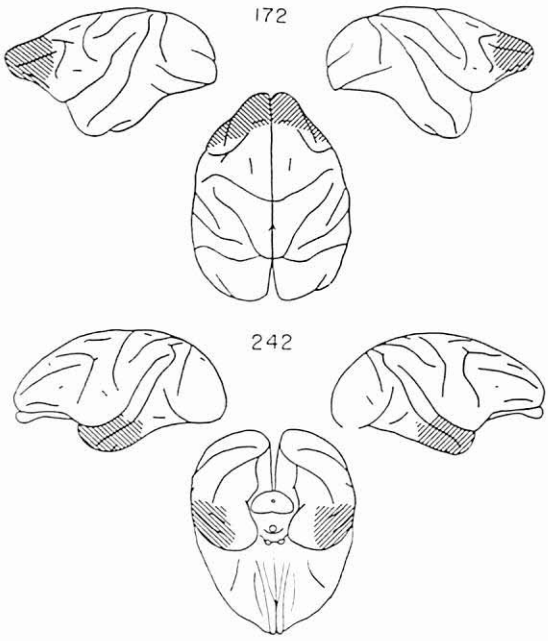

FIG. 2. The shaded areas indicate the extent of the cortical lesions as determined by reconstructions from serial sections. Insofar as possible the brain contours and sulcal patterns were traced from photographs.

ment will be made here of the extent of the damage.[3] All ablations were produced by subpial hydroaspiration.

Prefrontal lesions.[4] The lesions of monkey 172, shown in Figure 2, typify those of the prefrontal group. A total or near-total ablation of Brodmann's areas 12 and 9 was obtained in all cases. Area 8 was largely spared, although in animal no. 129 in the right hemisphere there was considerable encroachment of the superficial layers of area 8 to within about 1 mm. anterior to the bend of the arcuate sulcus. On the medial wall of all animals there was extensive damage to area 25 and those parts of area 24 ahead of the genu of the corpus callosum. In two animals the corpus callosum itself was slightly injured in its most anterior reaches. Large portions of the posterior orbital cortex remained. The olfactory sulcus and cortex medial to it were spared. The lateral ventricles were unopened, and the head of the caudate nucleus was not damaged by the primary lesions. In some monkeys there was, however, marked degeneration of small parts of the anterior tip of the head of the caudate, probably as a result of vascular involvement.

Temporal lesions.[5] In six of the animals the anterior half of the temporal neocortex was removed, as represented in Figure 2 by the reconstruction of the lesions of animal 242. In the remaining animals, monkeys 147 and 158, the ablation of the superior temporal gyrus was carried more dorsally and posteriorly. Ventromedially the extent of the lesions was subject to some variation from animal to animal but in general reached to about the limit of the neocortex.

Design

Three 20-min. sessions were given such that the second session followed the first by two days, and the third followed the second by two weeks. As in the preceding experiment, each session was divided into five successive 4-min. periods. For every period the index of locomotion was taken as the logarithm of the quantity, the number of beam interruptions plus 1.

The two-tailed F test of homogeneity of variance described by McNemar (7, pp. 229–231) was used to compare the over-all variability of the normal and prefrontal, normal and temporal, and temporal and prefrontal groups. A like set of comparisons among the mean scores was made with the distribution-free d statistic of Festinger (3). Parallel analyses of variance were carried out for the three groups.

Results

It was found that the variance for the prefrontal group (0.56) was lower than that for either the normal group (2.99) or the temporal group (2.46). The F ratios obtained in comparing these variances revealed that, while one could not reject the null hypothesis for the normal-temporal comparison, there were differences between the variances of each of these groups and the prefrontal group significant at the .002 level.

The geometric mean locomotion index of the prefrontal group (2.58) was higher than that of either the normal group (1.41) or the temporal (1.56). The differences between group means were not significant for the normals and temporals. The locomotion of the prefrontal group was, however, significantly greater than that of either the normal or the temporal group at the .01 level. Thus, for the groups participating in this experiment, there was an inverse relationship between the means and variabilities of locomotion scores.

A further analysis of this result is desirable. An examination of the graphic records obtained from individual animals shows that the typical patterning of locomotion in time is very different for the prefrontals as contrasted with normals and temporals. When the prefrontal animal moves in this situation, it paces continuously for a time; and between intervals of high activity there are short periods, never more than about 2 min. in length, when it re-

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[3] A detailed histological analysis of the lesions has been made and is available upon request to the Primate Laboratory, 29 Coyne Court, Madison, Wisconsin.

[4] The operations were performed by Dr. Paul H. Settlage of the Department of Anatomy.

[5] The operations were performed by Dr. Clinton N. Woolsey of the Department of Physiology.

TABLE 2

Summary of Analyses of Variance of Locomotion Scores

Source	Normal		Prefrontal		Temporal	
	df	Sig. of *F*	*df*	Sig. of *F*	*df*	Sig. of *F*
Sessions (S)	2	NS*	2	NS	2	NS
Periods (P)	4	.01	4	NS	4	.01
Animals (A)	20	.01*	4	NS	7	.01
S × P	8	NS	8	NS	8	NS
S × A	40	.01	8	NS	14	NS
P × A	80	NS	16	NS	28	NS
S × P × A	160		32		56	

* Tested against the S × A interaction.

mains immobile. As a result, the locomotion scores for the prefrontal monkeys are with few exceptions higher than the scores for the normals and the temporals. Moreover, since periods of prefrontal inactivity are relatively infrequent, the scores tend toward an upper limit. The normal or temporal animal's locomotion is distributed much more unevenly and desultorily, yielding scores which sometimes fluctuate markedly from period to period.

Frequency distributions of transformed scores for the three groups were plotted. Those for the normal and temporal groups were approximately bell-shaped. In contrast, the distribution for the prefrontal group was leptokurtic and negatively skewed. Therefore, a different transformation from that previously used was carried out on the raw scores of the prefrontal monkeys. This involved subtracting each raw score from 830 and taking the logarithm of the difference. The significance of 830 is merely that it is a constant found useful in making a normalizing transformation. The summaries of the analyses of variance, embodied in Table 2, show that sessions differences were significant for no group, thus confirming the result of Experiment I and indicating high stability of the locomotor reaction from session to session. It is remarkable that prefrontal animals did not show enough individual differences to contribute a significant source of variance, even though the lesions of the several animals in this group differed somewhat in extent. There were significant individual differences among both normal and temporal monkeys.

Although periods were not a source of significant variance for the prefrontal group, they were for the normal and temporal groups. In Figure 3 the points were obtained by calculating the mean period score for each group over the three sessions. For all groups, the locomotion scores are given in terms of mean log (beam interruptions + 1). An Alexander (1) test for trend was applied, and the results are in Table 3. Since for none of the groups was the *F* ratio yielded by testing Group Deviations from Linearity against Individual Deviations from Estimation greater than unity, straight-line fits of the data were deemed appropriate. For the prefrontal group, as indicated by the result of the test of Group Slope against Individual Deviations from Estimation, the slope of the least-squares straight line was not significantly different from zero. Although for both normals and temporals there is a significant component of Group Slope, the slope of the line for the temporal group is possibly attributable to individual variation. Under the conditions of these tests, there was a decrease in the rate of locomotion during the 20-min. testing session for the normal and temporal monkeys but no decrease for the prefrontal monkeys.

The analyses of variance showed significant individual differences in the normal and temporal groups. Coefficients of reliability were calculated on the data for the normal group. Comparison of sessions 1 and 2, sessions 1 and 3, and sessions 2 and 3 yielded *r*'s of .76, .75, and .82, respectively, each coefficient being significant at the .01 level. Therefore, the

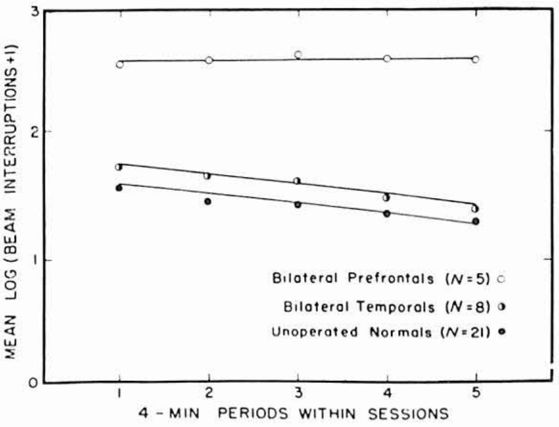

FIG. 3. Rate of locomotion of each group as a function of successive 4-min. periods within sessions.

TABLE 3

Results of Alexander Trend Tests on Locomotion Scores

Comparison	Normal		Prefrontal		Temporal	
	df	Sig. of *F*	*df*	Sig. of *F*	*df*	Sig. of *F*
Group dev. from linearity / Ind. dev. from estimation	3/60	NS	3/12	NS	3/21	NS
Group slope / Ind. dev. from estimation	1/60	.001	1/12	NS	1/21	.001
Group slope / Individual slope	1/20	.001	1/4	NS	1/7	NS

stability of the test is relatively high for intersession intervals of at least two weeks.

DISCUSSION

The pattern of locomotion clearly shown by normal monkeys during continuous exposures to an initially novel environment has been called "locomotor reaction decrement." Many terms have been operationally defined as the dropping out or lessening of movements in response to stimuli continuously or repeatedly presented; a few are "acclimatization," "negative adaptation," "accomodation," "stimulus satiation," and "exploratory drive." Reaction decrement has the advantages of not having other more customary usages and of not implying a possibly faulty explanation of the facts.

Harris's (4) comprehensive review of the literature on what we have called reaction decrement leads to the conclusion that it is characteristic of intact organisms over the entire phylogenetic range. The presence of broad morphological variations from phylum to phylum indicates a problem in specifying the structures which, at any given level, are most intimately involved in the mediation of this class of phenomena.

The present studies have demonstrated for the rhesus monkey, at least, that injury to the prefrontal brain is followed by profound modification of reaction decrement in the sphere of locomotion. In the situation employed here, not only is the rate of locomotor responding much higher and less variable for prefrontal as compared with normal monkeys, but also the rate is less subject to decay within sessions. A theory of the effects of prefrontal damage which considers the typical increase in locomotion only as the result of supposedly endogenous constant factors cannot well explain the observations, since it cannot predict the observed differences in decrement. A theory, such as that envisioned by Mettler (8), which would take into account differential reactivity of prefrontal animals to external stimulation is indeed required. These preliminary demonstrations obviously must be followed by more precise specification of the relevant stimulus parameters before the latter type of theory can be developed adequately.

SUMMARY AND CONCLUSIONS

In the present paper a method of assessing the locomotor behavior of monkeys placed in an initially novel, but thereafter constant, environment has been described. Application of the method led to the following results:

1. The normal rhesus monkey at first shows a high rate of locomotor responding. The rate of response decays in a negatively accelerated manner as a function of the length of time of continuous exposure, finally reaching an asymptote. Re-exposure to the situation after periods of from 24 hr. to two weeks results in no significant difference in the rate or temporal patterning of locomotion in groups of intact animals, although individual animals may vary in their relative level of response on successive days. In spite of this, coefficients of stability are found to be relatively high.

2. Brain operations involving bilateral removal of the neocortex of the temporal lobe with minimal damage to other temporal lobe structures have no statistically significant effect on locomotor reactions in this situation.

3. Bilateral ablations of the prefrontal area result in a rate of locomotion which is reliably

higher, less variable, and less susceptible to decay within sessions than is that of normal and temporal monkeys.

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THE EFFECT OF FLUID DEPRIVATION ON TASTE DEFICITS FOLLOWING CORTICAL LESIONS[1]

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Whether or not a deficit in taste discrimination follows cortical lesions in rats depends upon the type of discrimination test employed. If the usual two-bottle preference technique is used as a measure, the postoperative quinine thresholds may increase to thirty times the preoperative level after ablation of the cortical receptive zone of the chorda tympani and IXth nerves (1, 2). In this test the animal is presented with two bottles, one containing water, the other quinine solution. Under these conditions the amount of quinine consumed in a given period is inversely related to its concentration. When the concentration is sufficiently low, the animal shows no discrimination (i.e., drinks equal amounts of water and quinine solution). Following such lesions this null point is reached at a much higher concentration than preoperatively.

These operated animals, however, will display normal discrimination in what might be labeled a one-bottle, high-deprivation test. Here, the test fluid is presented for 1 hr. following 16 hr. of fluid deprivation. When strong concentrations of quinine are presented, the 1-hr. consumption is considerably less than the consumption of water for an equivalent test period. A concentration is reached where the consumption of water and quinine is equal. This null-point either remains the same or shifts to a lower concentration postoperatively (1).

There appear to be two variables in the experimental situations which might account for these differential results: the arrangement of the stimuli (one vs. two bottles), or the fluid deprivation state (16 hr. vs. none). Correlated with a deficit are both low deprivation and two bottles; with no deficit, one-bottle and high deprivation. Table 1 illustrates the combination of variables which produces deficits in operated animals and that which does not, and, further, it shows the two remaining combinations of variables which will be explored in the two experiments reported here.

If deprivation is the crucial variable, then operated animals should show a deficit on a one-bottle, low-deprivation test (Experiment I), but not on a two-bottle, high-deprivation test (Experiment II). If the stimulus arrangement is the factor, then the reverse would obtain.

METHOD

Experiment I. One-Bottle, Low Deprivation

The experimental animals were male albino rats, three to four months of age. The operative and histological procedures were described in an earlier paper (2). Each animal was housed in an individual cage to the front of which could be fastened one or two 100-cc. graduates equipped with rubber stoppers and matched drinking tubes. The experiments were conducted in an air-conditioned room with a constant temperature of 70° F. ± 4°.

As a check on the adequacy of the lesions, the animals were first run on the standard two-bottle, low-deprivation test followed by the one-bottle, low-deprivation test.

In determining the two-bottle thresholds, a given concentration of solution was presented for a total of 48 hr., the position being controlled by a double-alternation sequence. That is, the solution would be placed in the left bottle for 24 hr., then the right for the same period. The next concentration started on the right, then the left, etc. The position of the bottles and drinking tubes remained constant. By this procedure position habits and extragustatory cues were controlled.

A descending series of molar concentrations of quinine hydrochloride (QHCl) were used as follows: .0002, .00008, .00003, .00002, .000008, .000003, .000002. The threshold was defined as the last concentration at which the quinine intake constituted less than 25 per cent of the total fluid intake.

The procedure for the low-deprivation, one-bottle test was exactly the same as that used in the high-deprivation, one-bottle test (1) except that the solutions were presented for 24 hr. That is, after a five-day adaptation period when only water was presented, quinine solutions and water were presented on alternate days. Threshold was defined as the lowest concentration at which the test period intake of quinine

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[1] Part of this research was supported by a contract between the Office of Naval Research and Brown University. The research was completed while the author held a Corinna Borden Keen Research Fellowship from Brown University.

[2] Now at departments of Physiology and Psychology, University of Wisconsin.

TABLE 1

Combinations of Variables Investigated Previously and in the Present Experiments

Stimulus Arrangement	Deprivation State	
	High	Low
1 bottle	Normal	Exp. I
2 bottles	Exp. II	Deficit

TABLE 2

Schedule for the Two-Bottle, High-Deprivation Test

Period	Time	Fluid
Test	1 hr.	Tap water or QHCl solution
Rest	1½ hr.	None
Free access	5½ hr.	Water
Deprivation	16 hr.	None

TABLE 3

Postoperative Threshold Changes For Experiment I in Terms of Each Animal's Own Preoperative Threshold

Group	Animal No.	Stimulus Arrangement	
		2-bottle	1-bottle
Experimental	169	10.0	25.0
	167	10.0	3.8
	172	6.7	6.7
	166	3.8	0
	163	2.5	1.5
	162	2.5	1.5
Control	161	0	0
	171	0	0
	174	.67	0
	175	.67	.15
	170	.40	.38
	173	.38	.10

solution was less than the water intake on the preceding or following 24-hr. periods. The same descending series of quinine solution were used.

Following these preoperative tests, the animals were divided into two groups. The composite nerve area was removed bilaterally in the experimental animals. This area was constructed from the maps of six evoked potential recording experiments utilizing electrical stimulation of the IXth and chorda tympani nerves (2). The control animals were not operated. Postoperative tests were begun after an eight-day recovery period.

Thus, there were five stages in the experiment:

1. Two-bottle, low-deprivation test ($N = 18$).
2. One-bottle, low-deprivation test ($N = 18$).
3. Control Group ($N = 6$). Rest period, 8 days. Experimental Group ($N = 6$). Operation and recovery, 8 days.
4. Two-bottle, low-deprivation test.
5. One-bottle, low-deprivation test.

Experiment II. Two-Bottle, High Deprivation

Eighteen albino rats, 110 days of age were used. The animals were not run on the standard two-bottle, low-deprivation test in this case. Thus, there were only three steps in the experiment:

1. Determination of the two-bottle, high-deprivation QHCl thresholds ($N = 18$).
2. Control Group ($N = 6$). Rest period, 8 days. Experimental Group ($N = 6$). Operation (composite nerve area ablation) and recovery period, 8 days. Large Lesion Group ($N = 5$). Operation (large lesions of cortex including composite area) and recovery, 8 days.
3. Postoperative two-bottle threshold determination.

The order of presentation of the stimuli, concentra-

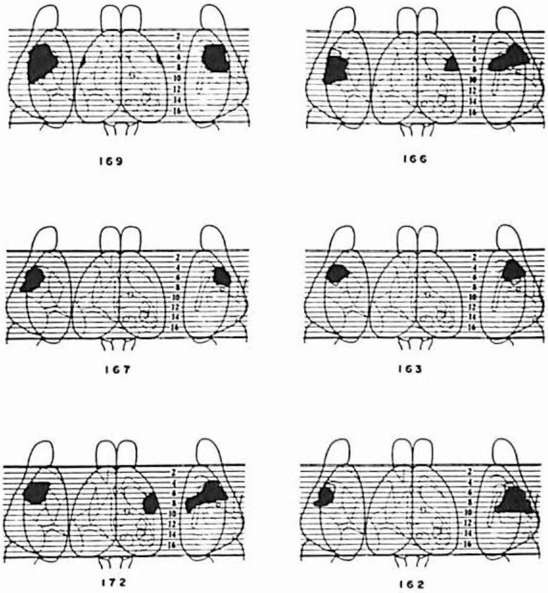

FIG. 1. Reconstructions of the lesions in the experimental animals, Experiment I. The composite nerve area is outlined.

TABLE 4

Postoperative Threshold Changes on the Two-Bottle, High-Deprivation Test (Experiment II) in Terms of Each Animal's Own Preoperative Threshold

Control		Experimental		Large Lesion	
*317	0.00	*315	0.00	*313	10.0
326	0.00	309	0.00	314	6.7
323	0.40	310	0.00	316	4.0
319	0.15	308	0.38	307	1.5
321	0.15	311	0.04	306	0.0
304	0.10	312	0.04		

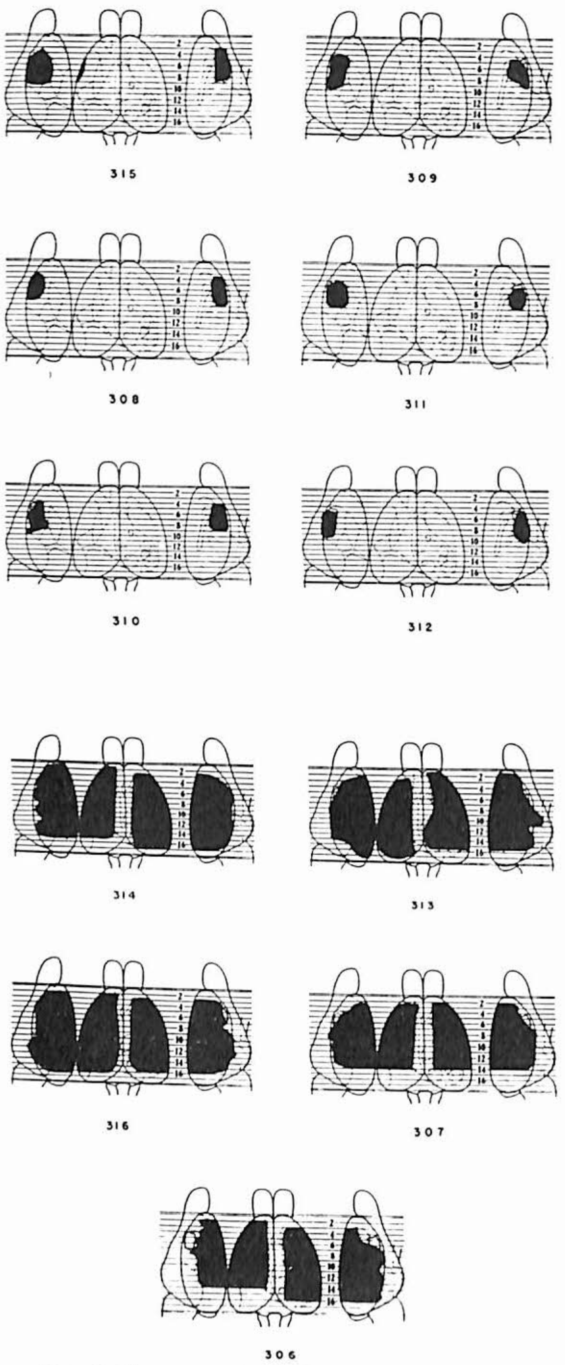

FIG. 2. Reconstructions of the lesions in the experimental and large lesion animals, Experiment II. The composite nerve area is outlined and can be seen in its entirety in the left hemisphere of no. 306.

tions, and definition of threshold were the same as for the two-bottle, low-deprivation test in Experiment I except that the solutions were presented for 1 hr. following 16 hr. of fluid deprivation. The 24-hr. schedule for the tests is indicated in Table 2. As indicated above, a third group of animals was included (Large Lesion Group) in which it was attempted to remove a large part of the neocortex bilaterally including the composite area.

RESULTS

Experiment I

Preoperative thresholds. The mean two-bottle, low-deprivation molar threshold was .000035; the one-bottle, low-deprivation, .000043. The Wilcoxon (4) test for paired replicates indicates there is no significant difference between these thresholds.

Postoperative thresholds. The postoperative results are presented in Table 3. In order to facilitate comparisons, these thresholds have been expressed in terms of the relative change from each animal's own preoperative threshold. Thus, 10.0 indicates the postoperative threshold increased to 10 times the preoperative level; 0, no change; and .10 indicates a decrease to one-tenth the preoperative level. The difference between the experimental and control groups is significant ($p < .01$) on both tests (Wilcoxon unpaired replicates test [4]).

The following generalizations can be made:

1. The thresholds for the Control animals either remained the same or decreased on both the one- and two-bottle tests postoperatively.
2. The thresholds for all the Experimental animals increased on the two-bottle test, and five of the six increased on the one-bottle test.

Histological. The lesion reconstructions (solid black) appear in Figure 1. The composite area, where any remains, is outlined. In three animals (no. 169, 167, 172) essentially all the composite area was removed bilaterally. In the other three animals various amounts of the area were left intact. It is interesting that there is some correlation between the size of the deficit and the amount of composite area destroyed. In animals 166 and 167 there was damage to the corpus striatum unilaterally, but there was no subcortical damage in the other four cases.

TABLE 5

Effect of Cortical Ablation with Various Combinations of Deprivation State and Bottle Arrangement

Stimulus Arrangement	Deprivation State	
	High	Low
1 bottle	Normal	Deficit
2 bottles	Normal	Deficit

Experiment II

Preoperative thresholds. The mean two-bottle, high-deprivation molar threshold was .000058. Since the animals were not run on the standard two-bottle, low-deprivation test, no direct comparison can be made. There is, however, no significant difference between these two-bottle, high-deprivation thresholds and either the one- or two-bottle, low-deprivation thresholds of Experiment I (Mann and Whitney *U* Test, 3).

Postoperative thresholds. The postoperative threshold changes are presented in Table 4. The results are summarized below:

1. The thresholds for both the Control and Experimental animals either remained the same or decreased postoperatively.
2. The thresholds of 4 of the 5 Large Lesion animals increased postoperatively.
3. The difference between the Large Lesion group and both the Control and Experimental groups is significant ($p < .01$, Mann and Whitney *U* test).

Histological. The lesion reconstructions appear in Figure 2. Essentially all the composite area was destroyed in three animals of the Experimental group (numbers 315, 308, 310), and varying amounts remained intact in the other three. In the Large Lesion group essentially all the composite area was destroyed in three animals (no. 314, 316, 313), approximately one-third remained bilaterally in no. 307, and nearly all the area survived in no. 306. The latter animal had no deficit. Destruction was confined to the cortex with minor invasion of subcortical white matter in a few cases.

DISCUSSION

The results as represented in the completed block indicate that the difference previously observed between the one-bottle, high-deprivation and the two-bottle, low-deprivation tests can be accounted for in terms of the single factor of fluid deprivation (Table 5).

Under low deprivation, regardless of the stimulus arrangement, ablation of the IXth and chorda tympani receptive areas produces increased thresholds. Under high deprivation, the ablation has no measurable effect.

If large lesions are made which include not only the composite area, but most of the rest of the neocortex as well, then deficits can be demonstrated under high-deprivation conditions. Whether this is a "mass" effect or whether there is a locus for a high-deprivation deficit cannot be determined from these animals. It is not even certain that the composite area must be included in these lesions if a deficit is to follow, although the data of animals 306 and 307 would suggest this conclusion. It is evident, however, that as the deprivation conditions change, the neural structures necessary for normal discrimination also change. Thus, taste discrimination, even under these relatively restricted conditions, is not a unitary process which can be referred to a single "taste" area. Localization of function, at least as far as taste is concerned, must be in terms of the experimental variables rather than some abstracted discriminative capacity.

SUMMARY

Whether ablation of the chorda tympani and IXth nerve receptive area of the cortex produces deficits in taste discrimination depends upon the type of discrimination test employed. Increased thresholds will follow such lesions on either a one- or two-bottle test if the animal is under conditions of low fluid deprivation. Under high fluid deprivation (16 hr.), the postoperative performance is normal with either a one- or two-bottle test. High-deprivation deficits can be produced, however, if most of the neocortex is removed in addition to the taste nerve area. It is concluded that the taste nerve area is necessary for normal taste discrimination only under conditions of low fluid deprivation and that other cortical areas are involved in discrimination when fluid deprivation is high.

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THE EFFECT OF ADRENALINE ON A CONDITIONED AVOIDANCE RESPONSE[1]

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The acute fear "paralysis" which occurs in some soldiers when going into combat might be associated with the excessive discharge of adrenal medullary hormones. Experiments conducted in this laboratory have shown that adrenaline suppresses movements produced by stimulation of the motor cortex,[2] and it is possible that this depression of higher neural functions is due to a direct central action of the drug. The present experiment, while demonstrating a profound suppression of conditioned behavior with large epinephrine doses, does not support a central depressing action.

There are few studies in the literature concerning the effect of adrenaline on learned behavior. A beneficial effect on maze learning in the rat was reported (1) from the intraperitoneal injection of a very low dose (0.5 cc. of a 1:500,000 solution). In the dog, 0.1 mg. adrenaline caused an increase in the intensity of a conditioned response, while a larger dose was inhibitory (5). The drug (dose not stated) impaired the performance of dogs having excitatory and inhibitory conditioned responses (2).

The following experiment was undertaken to determine the effect of massive doses of adrenaline on the performance of a learned response. Rats learned a conditioned avoidance response, and their performance on the task was measured after administration of adrenaline. In order to determine whether any observed effects were central or peripheral, the performance of adrenaline-injected animals was also studied after pretreatment with the adrenergic blocking agent, dibenzyline (4). A central action would be suggested if any changes in performance which occurred with adrenaline were also present when the peripheral effects of the drug were blocked by dibenzyline.

METHOD

Subjects

The *S*s were 30 male albino rats from the Sprague-Dawley strain. The animals ranged in weight from 110 to 260 gm.

Apparatus

The apparatus was a modified Skinner box with a grid floor. The box measured 19 by 19 by 19 in., and had one glass wall to permit observation. It was equipped with a 1- by 4-in. wooden pedal which was located on the back wall, 2 in. from the floor. The conditioning stimulus, a 40-w. light, was inserted through the top of the box. The grid was composed of 1/8-in. copper bars, placed 1/2 in. apart. The current was delivered by a hand-operated switch. The pedal was wired and connected with a separate switch so that shock could be administered either through the grid or through the pedal. The shock delivered was 100 v. through a fixed resistance of 220,000 ohms.

Procedure

Initial training. The initial training was carried out in the following manner. The rat was placed in the box and allowed to explore for 10 min. Current was then delivered through the grid, and *S* was trained to place its front paws on the pedal to escape the shock. This was accomplished by giving the animal several trials, 1 min. apart, during which the shock was turned off as soon as *S* approached the pedal. When *S* learned to run toward the pedal to escape, the shock was continued until *S* touched the pedal with its forepaws. As soon as the rat associated the pedal with reinforcement, it tended to remain on it. The *S* was allowed to stay on it for 30 sec.; *S* was then lifted off and placed in the front of the cage. After another 30 sec. the next trial was begun. This training was continued until *S* responded correctly within 5 sec. of the onset of the shock on five consecutive trials. There was a large amount of variation in the number of trials necessary to meet this criterion, as the rapidity of learning depended greatly upon how soon the animal discovered the pedal.

The light was then paired with the shock, and the animal was trained to respond to the light to avoid the shock. The light preceded the shock by 5 sec. and was left on until the response occurred. If *S* placed its forepaws on the pedal within this 5-sec. period, it avoided the shock. It was permitted to remain on the pedal for 30 sec. and was then lifted off, and the next trial was given after another 30 sec. If *S* touched the pedal before the onset of the light stimulus, it was shocked through the pedal. If *S* did not respond to the shock after 30 sec. of stimulation, the shock was dis-

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[2] S. Ochs. Personal communication, 1954.

continued and a new trial was begun 30 sec. later. Actually, this problem did not arise during the training trials, but occurred during the test trials of some of the adrenaline-treated animals.

All the *Ss* were given the escape training plus 30 avoidance trials in one session on day 1. Trials were recorded in blocks of 15, and each animal was given 15 trials beyond the point where it had made 10 avoidance responses in the last block of 15 trials. No more than 45 trials were given on day 2. Most of the animals had met the criterion by this time; those which had not were given additional trials (no more than 45 per day) on days 3 and 4. The number of preliminary trials necessary ranged from 45 to 105. Most *Ss* needed only 45 to 60 trials.

Test trials. The *Ss* were divided into three groups, matched individually on the basis of the number of training trials necessary to meet the criterion, and were tested under one of the following conditions:

Group I: Control ($N = 10$)
Group II: Adrenaline ($N = 10$)
Group III: Dibenzyline and Adrenaline ($N = 10$)

The control animals were given 60 successive trials beginning 2 hr. after the last training trial. The *Ss* in Group II were injected subcutaneously in the nape of the neck with 0.6 mg/100 gm adrenaline in oil (Abbott, 1:500 solution) 90 min. after the last training trial; they were then given 60 test trials beginning ½ hr. after the injection. Those in Group III were given a subcutaneous injection of 0.4 mg/100 gm dibenzyline (1 mg/cc solution) immediately after the preliminary trials. They were injected with 0.6 mg/100 gm adrenaline in oil 90 min. later, and their test trials followed the adrenaline injection by ½ hr.

RESULTS

The means and *SD*'s of the number of conditioned responses in the 60 test trials are shown for the three groups in Table 1. The column headed "Avoidance Responses" refers to the frequency of response to light. Since, in some instances, the adrenaline-treated animals failed to respond to the shock in the 30 sec. allowed, the column labeled "Total Responses" was included to show the number of responses to shock *or* light. Comparison of the means shows that the injection of adrenaline caused a striking decrease in the frequency of avoidance responses (13.0/60 as compared with control value of 56.2/60), and a small decrease in the mean number of total responses (49.9/60 versus 60/60). In both instances dibenzyline provided complete protection against the loss of the conditioned response.

TABLE 1

Mean Number of Conditioned Responses
($N = 10$ each group)

Group	Avoidance Responses		Total Responses	
	M	*SD*	M	*SD*
Control	56.2	2.0	60.0	0.0
Adrenaline	13.0	12.6	49.9	14.1
Adrenaline and dibenzyline	55.9	2.9	60.0	0.0

An analysis of variance for matched groups, when applied to the number of avoidance responses, yields an F of 126.3, which, for 2 and 18 *df*, is significant at the .001 level of confidence. An analysis of variance of the total responses gives an F of 4.6, which is significant at the .05 level of confidence. It can be seen by inspection of the means that, for both avoidance and total responses, it is the adrenaline-treated group which differs significantly from the other two groups, and that the difference between the means of the controls and the dibenzyline-adrenaline animals is not significant.

DISCUSSION

There are several possible explanations for the depressed performance of the adrenaline-treated animals. First, there is the possibility that the *Ss*' vision was affected by vascular changes in the eye, and that they did not respond because they could not see the light or the pedal. This is not likely, as it was observed that most of the animals gave anticipatory responses to the light long after their conditioned avoidance responses had dropped out and, in some cases, after the loss of the escape response. These anticipatory responses consisted of startle reactions, turning in the direction of the pedal, and sometimes approaching the pedal.

The second explanation is that the drug, acting centrally, interfered with performance through an effect on either retention or on motivation. In the latter case the loss of the escape response would indicate a reduction in the primary pain drive, while the loss of the avoidance response would suggest a decrease in the fear drive which has been postulated to motivate such responses (3). Although the possibility of a central action cannot be completely ruled out, two facts argue strongly against it: (*a*) Dibenzyline, which has no known central effects, protected against the loss of the conditioned response. (*b*) The general behavior of the adrenaline-treated animals suggested a peripheral action.

The most satisfactory explanation for the effect of adrenaline on the conditioned response is that the depressed performance of the experimental animals was due to a general effect of the drug on activity and motor capabilities, rather than to a specific action on the central nervous system. The adrenaline made the animals very ill—they were weak and lethargic and appeared to experience great difficulty in performing the task. They moved slowly, and the latency of the escape response was frequently prolonged. None of these symptoms was present in the *S*s in which the peripheral effects of adrenaline were blocked by dibenzyline, and their performance on the task was not impaired. Thus, the loss of the conditioned response in the adrenaline-treated animals was probably part of a general depression of activity arising from the peripheral effects of the drug, and does not indicate a specific action of adrenaline on the central nervous system.

SUMMARY

Thirty rats were taught a conditioned avoidance response and were then tested under one of the following conditions:

Group I: Control
Group II: 0.6 mg/100 gm adrenaline in oil
Group III: 0.4 mg/100 gm dibenzyline plus 0.6 mg/100 gm adrenaline

It was found that the adrenaline caused a sharp decrease in the frequency of the conditioned avoidance response and a slight decrease in the frequency of the escape response. Dibenzyline furnished complete protection against this loss. Several interpretations of these results are discussed.

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